



Validation of a classification protocol: meeting the prospect requirement and ensuring distinctiveness when assigning forest development phases

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Keywords

Development stages; Distinctiveness; *Fagus sylvatica*; Forest development cycle; Gap dynamics; Primeval beech; Prospect requirement

Abbreviations

TC = Tabaku classification; DBH = diameter at breast height; G/R = gap/regeneration phase; E = establishment phase; EO = early optimum phase; MO = mid optimum phase; LO = late optimum phase; T = terminal phase; D = decay phase; P = plenter phase; CPA = canopy projection area; MaxD = maximum DBH; DS = deadwood share; MeanD = mean DBH; NQD = normalized quartile DBH difference; PSH = proportional stand height.

Nomenclature

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Introduction

Classification typologies can be helpful both for formulating hypotheses about the ecological processes shaping the different types (i.e. classes) to be classified and for developing subsequent 'close to nature' management strategies (De Cáceres et al. 2015). For instance, emphasis has been

Abstract

Aims: Evaluation and modification of a classification protocol for delineating development phases of the beech forest life cycle (Tabaku, Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und-Wirtschaftswäldern, 2000).

Location: The Uholka-Shyrokyi Luh primeval beech forest, Carpathian Biosphere Reserve in the Ukrainian Carpathian Mountains.

Methods: The classification protocol was evaluated by examining the requirements for each type based on the literature and empirically assessing the suitability of the typology resulting from applying it to non-overlapping 156.25 m² grid cells superimposed on a 10-ha stem-mapped old-growth European beech stand. Modifications were proposed and the modified protocol applied to the 10-ha old-growth stand and evaluated using permutation tests to assess the distinctiveness of primary attributes among types in the resulting typology.

Results: We found a consistent bias in the classification protocol resulting from a failure of the prospect requirement: the compound classification rule rendered it virtually impossible for grid cells to be assigned to the Late Optimum phase. The proposed modified protocol alleviates this problem and was found to result in distinct types with statistically significantly different mean values for many primary attributes.

Conclusions: Interpretations of a purported 'signature texture' for old-growth beech forests dependent on the absence of the Late Optimum phase when using the original classification protocol require reconsideration. The proposed modified protocol would be less susceptible to this bias, but caution is still advised, given the inherent constraints of the classification protocol at small scales.

placed on assigning and tracking forest stand structures and their associated development types as surrogates for biodiversity monitoring (Pressey 2004; Corona et al. 2011). However, successful application of a classification typology depends upon the classification protocol meeting general requirements for accepting the usefulness of the typology resulting from a given classification approach (De

Cáceres et al. 2015). For example, the classification approach should encompass the full range of variation of the ecosystem components being classified (i.e. comprehensiveness) and/or types should be distinct with respect to the primary classification attributes (i.e. distinctiveness; De Cáceres et al. 2015). In the case of assigning development phases (= types) to forests, at the very least the classification protocol must capture the salient ecological processes thought to shape the development phases (cf. Leibundgut 1959, 1993; Korpel' 1995) (i.e. representativeness, Peck et al. 2015). Representativeness is typically achieved by using primary attributes thought to be linked to the processes associated with each phase of the beech forest life cycle (Leibundgut 1993; Korpel' 1995). Further, logic dictates that the sequence of assignment rules be structured such that it is theoretically possible for all development phases to be assigned as intended (the prospect requirement); i.e. the rules must be sufficiently consistent across the hierarchy (cf. Mayr & Bock 2002) that the criteria for a given type are mutually compatible.

As patches of forest progress through the forest life cycle, the ecological processes dominating each period leave behind telltale structural signatures. Periods associated with regeneration processes thus have lower total biomass, which has been found to peak during periods of growth and decline with increasing mortality (Watt 1947; Meyer 1952; Korpel' 1995; Emborg et al. 2000; but see Zenner et al. 2015b). This association between process and structure has led to the delineation of developmental stages and structural phases on the basis of stand structure (Leibundgut 1978; Korpel' 1995; Meyer 1999). In addition to total biomass, the structural attributes taken as indicators of different phases of the forest life cycle have included the presence of regeneration (Rall 1990; Heurich 2006) or gaps (Emborg et al. 2000; Tabaku 2000), tree species richness (Rall 1990), layering of the canopy (Heurich 2006), deadwood (Tabaku 2000; Heurich 2006), measures of heterogeneity in tree size structure (Tabaku 2000) and the ratio of increment:mortality (Meyer 1999). Objectively assigning patches of forest to development phases can therefore be achieved using a set of assignment rules that draws on an expert-based membership rule definition (*sensu* De Cáceres & Wiser 2012) in which criteria for assignment are defined *a priori* from expert knowledge (e.g., Král et al. 2010; Huber 2011). Perhaps because the first classification protocols based objectively on data, rather than subjective field assessment, were reported only in the regional literature (see Tabaku 2000; Winter & Brambach 2011), implementation has been slow. Among the first to have been developed (Meyer 1999) and applied (Tabaku 2000; Drößler & Meyer 2006) is the classification method of Tabaku (2000) (hereafter the TC method).

The first serious effort to broaden awareness of objective classification protocols developed for investigating patch dynamics in old-growth European beech (*Fagus sylvatica* L.) forest focused on expanding, rather than evaluating, the original protocols (Winter & Brambach 2011). For example, the TC method uses a set of dichotomous compound assignment rules for seven primary structural attributes [canopy projection area (CPA), deadwood share (DS), tree regeneration and various metrics reflecting the tree size distribution] to assign development phases to small (156.25 m²) square grid cells superimposed on a larger stem-mapped forest area. The proportion of forest area belonging to each phase in the resulting typologies has been interpreted to reflect the duration or likelihood of given developmental periods (e.g., Schütz 2001) or to indicate status, such as the near absence of the late optimum phase being hailed a signature texture of primeval old-growth beech (Tabaku 2000; Drößler & Meyer 2006). However, the validity of the classification protocol, and therefore the conclusions drawn from it, has never been systematically evaluated. Although Winter & Brambach (2011) proposed revisions to the TC method, they were derived deductively (with scant justification) rather than empirically, and neither the original nor their revised TC method has ever been assessed for suitability as a classification protocol. Further, while Winter & Brambach (2011) expanded the application to larger spatial scales, they ultimately concluded that the original small spatial scale was suitable for capturing fine-scale forest development phases reflective of structural microhabitats.

Nonetheless, concerns about the validity of the TC method (even as modified by Winter & Brambach 2011) remain. Some suggestions for improvement have related to measurement protocols for primary attributes, such as the proposal that one of the structural attributes (crown projection area) be calculated based on single crown coverage rather than multiple coverage of overlapping crowns (Drößler & Meyer 2006). Another, and perhaps more fundamental, concern relates to the complete absence of one of the sequential development phases (Late Optimum) in old-growth beech forests for which typologies have been developed (Tabaku 2000; Drößler & Meyer 2006), which is inconsistent with observations fundamental to the development of the sequential classification approach and results from other classification methods that report at least a low frequency of the Late Optimum stage in primeval beech stands (e.g., Korpel' 1995; Král et al. 2010, 2014a). In the absence from the literature of any plausible ecological mechanism for skipping a development phase within the forest life cycle, we hypothesize that the failure to observe the Late Optimum development phase using the TC method could be due to a logical error in the classification protocol that violates the prospect requirement.

The suitability of the resulting typology for the purpose of delineating development phases can be evaluated (i.e. validated) by examining the requirements for each type based on the literature (De Cáceres & Wiser 2012). In addition, classification protocols can be evaluated using internal criteria such as distinctiveness (De Cáceres et al. 2015). The goals of this paper therefore were to (1) evaluate the validity of the TC method (i.e. check the prospect requirement) and (2) propose a Modified TC method and evaluate its distinctiveness when applied to assign forest life cycle development phases within a 10-ha portion of an old-growth European beech forest reserve in the Carpathian Mountains of southwestern Ukraine.

Methods

Study area

Sampling was conducted within the primeval Uholka-Shyrokyi Luh forest, which is part of the Carpathian Biosphere Reserve. Situated in the Ukrainian Carpathians, the reserve lies within a highly fragmented massif that consists mainly of flysch formations of the Cretaceous and Paleogene periods, with Jurassic limestone, calcareous conglomerates, marls and sandstone (Hamor & Brändli 2013). The climate is temperate, with a mean annual temperature of 7.7 °C (−2.7 °C in January and 17.9 °C in July) and a mean annual precipitation of 1134 mm. There is no historical evidence that the Uholka-Shyrokyi Luh forest has ever been cut and the almost pure European beech (97.3%, by basal area) forest shows typical structural features of an old-growth forest (Commarmot et al. 2013; Hobi et al. 2015a). The forest is thought to be dominated by a small-scale disturbance regime, with canopy gaps mainly <200 m² (Hobi et al. 2015b).

Data collection

In 2000, a 10-ha (200 m × 500 m) plot was established in the Uholka portion of the forest (48°16' N, 23°37' E, centre coordinates) on an exposed southeast slope of 20–40% at an altitude of 700–800 m a.s.l. (Commarmot et al. 2005). Within the plot, all live and dead trees (standing and lying) with a DBH ≥ 6 cm were marked and mapped, and their DBH, species and the presence of a stem bifurcation were recorded. All snags and a random subsample of 200 live trees distributed throughout the plot were measured for tree height and the upper stem diameter 7 m above the ground. After Michailoff (1943), heights for all trees were estimated based on non-linear regressions between DBH and height (H) from the subsample ($H = 1.3 + 53.67 \times \exp(-18.36/DBH)$ with $R^2 = 0.93$ and RMSE = 3.87 m). Crown length and four crown radii in the cardinal directions were measured for each standing

tree in the subsample to estimate crown projection areas based on a non-linear regression between DBH and crown diameter (KD) [$KD = \exp(0.69302 + 0.39183 \times \ln(DBH))$ with $R^2 = 0.55$ and RMSE = 1.29 m]. In 2010, re-measurements of DBH were taken and new trees (ingrowth to 6 cm DBH) were stem-mapped; the 2010 measurement data were used in this study.

Classification approach and protocol

The core of the basic stand development cycle is the recognition that the dominant ecological process, which has the largest net influence on total live biomass, leaves a characteristic structural signature that can be used to quantify patch dynamics and spatially demarcate development phases (e.g., Leibundgut 1959; Mayer 1982; Korpel' 1995; Emborg et al. 2000). The growing-up stage, dominated by regeneration and growth processes, is characterized by steadily increasing biomass, which culminates in the optimum stage and then declines through the decay stage (Leibundgut 1959, 1978; Korpel' 1995; Meyer 1999; Tabaku 2000; Drößler & Meyer 2006). These primary phases are divided into nine development phases (cf. Tabaku 2000; Drößler & Meyer 2006) on the basis of the structural hallmarks of the dominant ecological processes previously identified by experts in the field (Table 1): Gap (G), Regeneration (R), Establishment (E), Early Optimum (EO), Mid Optimum (MO), Late Optimum (LO), Terminal (T), Decay (D) and Plenter (P).

The TC method objectively assigns patches of forest to these expert-defined development phases using a set of assignment rules evaluated at the 156.25-m² scale (Tabaku 2000). This size, which is equivalent to the crown projection area of a mature (70 cm DBH) beech tree (Meyer 1999), corresponds to the smallest spatial scale at which development phases have been assigned using the TC method (e.g., Tabaku 2000; Drößler & Meyer 2006). The 10-ha plot was thus first divided into non-overlapping adjacent grid cells with a mesh size of 12.5 m × 12.5 m ($N = 640$ grid cells).

This classification protocol then applies a simple decision tree using compound membership rules for primary structural attributes to divide the continuous forest life cycle into the nine development phases (Tabaku 2000). The primary attributes computed for each grid cell include: (1) CPA, i.e. the proportion (per cent) of a grid cell area covered by the overlapping crown projection of all live trees; (2) the maximum DBH (MaxD) of standing trees within a grid cell; (3) the DS, i.e. the proportion (per cent) of the total (live and dead) volume in a grid cell comprised of dead trees; (4) the mean DBH of standing live trees (MeanD); (5) the normalized quartile DBH difference (NQD), which assesses variability in tree sizes as 100 times

Table 1. Characteristics of the development phases of the beech forest life cycle classification approach (adapted from Leibundgut 1993; Korpel' 1995 and Tabaku 2000).

Development Phase Type	Characteristic Processes
Gap (G)	Overstorey mortality opens the canopy such that gaps (unstocked areas) become the dominant feature; gaps are either closed by crown expansion from neighbouring trees, filled with new or older advance regeneration that is released, or remain open [delineated by Tabaku (2000); previously part of the Decay phase]
Regeneration (R)	Understorey tree regeneration becomes widespread, while overstorey mortality continues
Establishment (E)	Mortality finally eliminates the remaining overstorey trees, permitting seedlings to grow into an established sapling cohort
Early Optimum (EO)	Vigorous growth of the sapling cohort increases stocking and closes canopy gaps, precluding further regeneration
Mid-Optimum (MO)	Density-dependent mortality decreases, but continued vigorous growth of the new cohort increases stocking until the new cohort forms a closed canopy and becomes dominant (i.e. is now the overstorey)
Late Optimum (LO)	Growth maintains the closed canopy overstorey with maximum stocking
Terminal (T)	Density-independent mortality of individuals and groups of overstorey trees begins to create snags and mostly single-tree gaps, reducing stocking
Decay (D)	Overstorey mortality reduces stocking and creates larger canopy openings, many snags and high coarse woody debris, and conditions conducive to regeneration
Plenter (P)	Characterized by a strongly differentiated, multigenerational structure, this phase was considered by Leibundgut (1993), Korpel' (1995), and many others to be non-sequential in the beech life cycle

the size difference (DBH) of the tree of the 75th percentile and the 25th percentile divided by the median DBH in each grid cell; (6) the proportional stand height (PSH), i.e. the proportion of the height of the tallest tree in a grid cell relative to the tallest tree in the stand (47.9 m); and (7) the proportion of the plot covered by tree regeneration (REG). The decision tree uses primary attributes to dichotomously separate phases if certain thresholds are not met or exceeded: (1) the CPA (<30%) uniquely identifies the G phase; (2) DS ($\geq 30\%$) segregate the R, E, EO and D phases that are further classified by REG and MeanD; (3) PSH ($\geq 85\%$) separates the T phase from the three Optimum (O) phases; (4) NQD (>100) separates the P phase from the T and the three Optimum phases; and (5) MaxD distinguishes among the three O phases (EO if the MaxD < 40 cm, MO if $40 \text{ cm} \leq \text{MaxD} < 60 \text{ cm}$ and LO if the MaxD is $\geq 60 \text{ cm}$).

Before each grid cell could be classified into development phases following the decision tree, three minor adaptations to the TC method were necessary. First, because regeneration (REG) was not spatially explicitly mapped for the entire plot and hence unavailable for use in the decision tree, the G and R phases were combined into a single phase (G/R) (Fig. 1a). Second, we computed the DS on a basal area rather than a volume basis because smaller lying coarse woody debris (i.e. branches and parts of stems) was not spatially explicitly mapped. DS is thus defined as the basal area of dead standing and lying trees as a percentage of the total basal area of all living and dead trees over 6 cm DBH within a grid cell. The effect of this modification is expected to be minor as basal area and volume were highly correlated ($r > 0.995$) in this study. Finally, because the TC method of calculating CPA ignores the facts that some of that projected crown area may extend outside the grid cell

and that the projected crown areas of different trees often overlap within a grid cell, Drößler & Meyer (2006) proposed that computing CPA based on a single crown layer rather than overlapping crown layers could alleviate the tendency toward underestimation of the areal proportion in gaps extrapolated from the proportional area assigned to the gap phase. We thus computed CPA by summing CPAs within a grid cell such that overlapping crown areas were only incorporated once, and included crown areas projecting into the grid cell from trees in neighbouring cells while excluding those projecting outside of the cell from trees rooted within the cell, thus bounding the CPA estimate between 0% and 100%. The effect of this modification was a decrease in the relative abundance of the G/R phase, from 5.6% in the TC multi-layered method to 3%, in favour of the E phase that increased from 7.9% to 10.5%.

Classification requirements

The TC method classification protocol (Fig. 1a) was evaluated by examining the requirements for each type based on the literature. The absolute threshold values of the primary attributes (e.g., MaxDBH value of 60 cm) used in the protocol correspond to reported diameter distributions from previous research that has shown that beech trees can easily achieve this tree size (Korpel' 1995; Tabaku 2000; Commarmot et al. 2005; Holeksa et al. 2009; Kucbel et al. 2012). This is also true for the relative abundance thresholds (e.g., 30% CPA, 30% DS) (Tabaku 2000; Drößler & Meyer 2006; Winter & Brambach 2011). This overlap in attributes demonstrates that these thresholds are widely attainable in old-growth European beech forests (Christensen et al. 2005; Westphal et al. 2006). Given that the average attributes of the Uholka old-growth forest

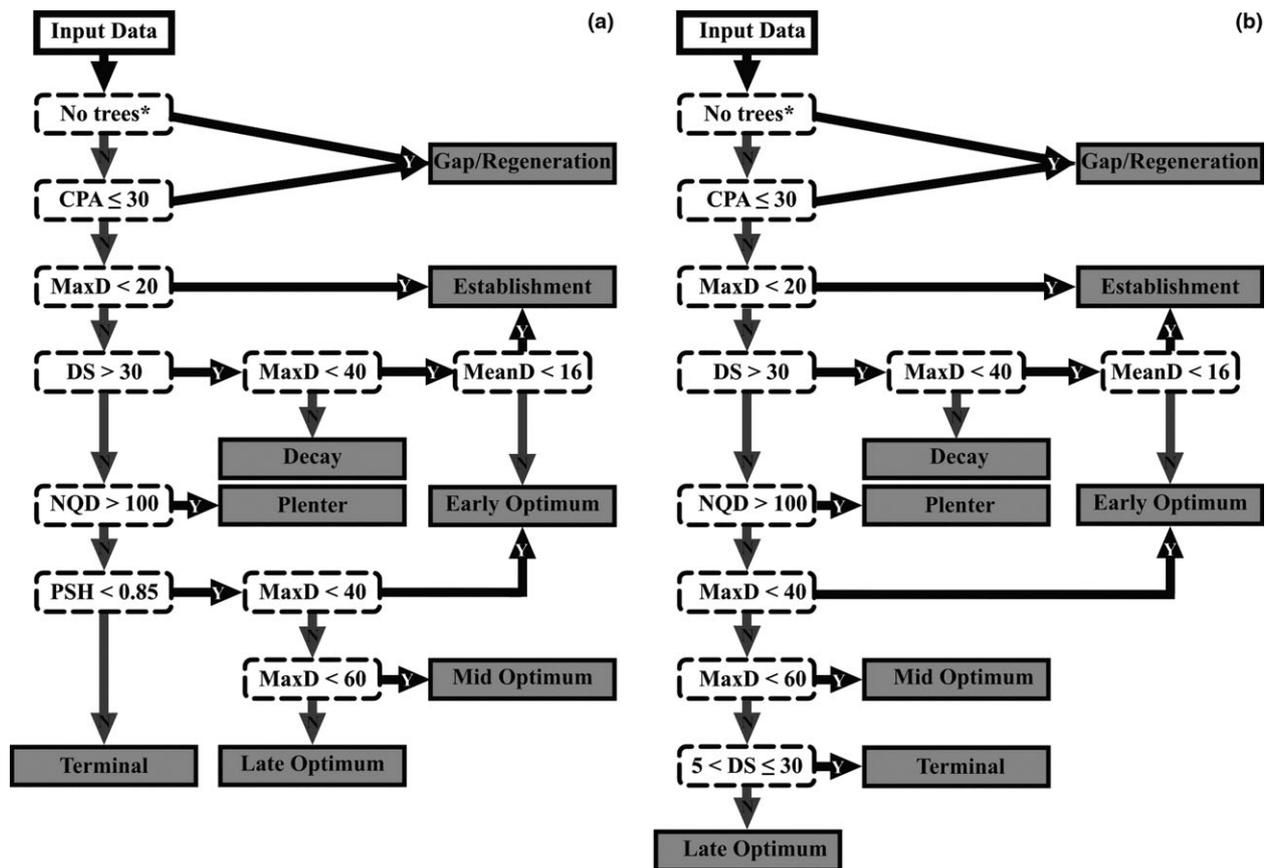


Fig. 1. Decision tree and intensive class definitions for assigning development phases using classification protocols (a) adapted from Tabaku (2000) (TC method) and (b) for the Modified TC method. Each primary attribute is evaluated as a dichotomy, assigning grid cells differentially if the criterion is met (Y, black arrows) or not met (N, grey arrows). CPA, canopy projection area; MaxD, maximum DBH; DS, deadwood share; MeanD, mean DBH; NQD, normalized quartile of DBH; PSH, proportional stand height. * ≥ 6 cm DBH.

(Commarmot et al. 2005; Hobi et al. 2015a) are similar to those reported for other beech old-growth forests (Pruša 1985; Korpel' 1995), use of these thresholds was also deemed appropriate for the current classification.

Suitability of the typology

To investigate if the TC method met the prospect requirement, we examined each compound assignment rule for consistency across the decision tree (Fig. 1a). To facilitate comparison with the literature, we quantified the development phase distribution resulting from the TC method classification as the proportion of area assigned to each type. We found that most compound rules allowed for the assignment of the intended phase: e.g., it is possible for a plot to have both $DS > 30$ and $MaxD > 40$ (Decay); both $DS > 30$ and $NQD > 100$ (Plenter); $NQD < 100$ and $PSH > 0.85$ (Terminal); and $PSH < 0.85$ and $MaxD < 40$ (Early Optimum) or < 60 (Mid Optimum). However, upon noting that no grid cells in the current study achieved

$PSH < 0.85$ and $MaxD > 60$ (and thus none were assigned to the Late Optimum phase), we explored the relationship between tree height and DBH in the current study and the literature. To determine if this indicated a local or a global failure of the prospect requirement, we compared the predicted height at 60 cm DBH to the reported maximum tree heights using the DBH–height regression equation for the current study and published regression equations from primeval beech stands (Tabaku 2000; Drößler & von Lüpke 2007; Holeksa et al. 2009). We found that the PSH attribute threshold introduced a bias of preferential assignment to the T rather than the LO phase: the regression relating DBH to tree height in the current study indicated that a tree with a DBH of 60 cm or more (i.e. the threshold for the LO phase) *always* exceeded a PSH of 85% (Fig. 2), such that the assignment of a grid cell to the LO phase had a zero probability because it was impossible to simultaneously exceed the 60 cm DBH threshold and stay below a PSH of 85%. Such grid cells were instead always assigned to the T phase. Very few exceptions were found when we

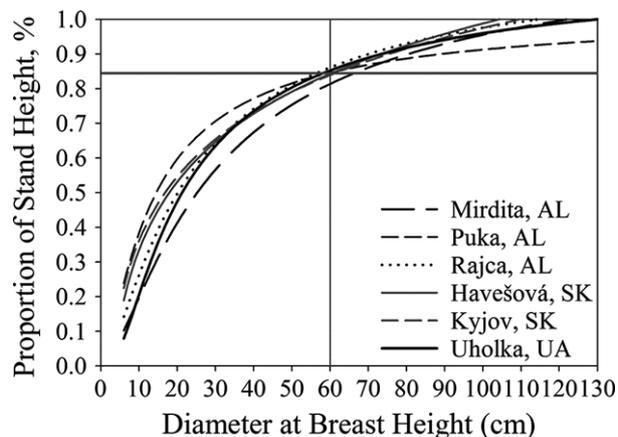


Fig. 2. The relationship between tree DBH and estimated values (based on the regression of tree height on DBH) for the proportion of stand height (PSH) criterion from the original TC method for the current study (Uholka, solid black line) and for five other old-growth reserves previously reported in the literature for Albania (AL; Tabaku 2000) and Slovakia (SK; Drößler & von Lüpke 2007). Note that very few trees from any site would have both a PSH < 85% and a DBH > 60 cm (i.e. the lower right quadrant).

computed the PSH of predicted tree heights from the regression equations for five other primeval beech stands in Albania (Tabaku 2000) and Slovakia (Drößler & von Lüpke 2007; Holeksa et al. 2009; Fig. 2). We thus conclude that this likely represents a global failure of the prospect requirement by the TC classification protocol.

To resolve the violation of the prospect requirement, we modified the TC method (hereafter the Modified TC method) by omitting the PSH criterion from the decision tree and, instead, broadening the use of the DS criterion to distinguish between the LO and T phases (Fig. 1b). Previously, the DS criterion primarily distinguished D (DS \geq 30%) from the O, T and P phases (DS < 30%). We chose, for demonstration purposes, a DS cut-off value of 5% to further distinguish between the LO (<5% DS) and T (\geq 5% DS and <30%) phases. This modification resulted in the reclassification of five grid cells (0.8%) from the T to the MO phase and of 197 grid cells (30.8%) from the T to LO phase (Table 2).

Due to significant departures from normality, testing for differences in the average values of the primary attributes across the 640 grid cells assigned to development phases using the Modified TC classification protocol was done using permutation tests (Good 2013). The average value of each attribute in each development phase was computed, followed by a random assignment of attribute values to development phases, and then the permuted mean was calculated. This process was repeated 10000 times, and the observed means compared to the permuted means. Differences between development phases were considered significant at the $\alpha = 0.05$ level. The Holm-Bonferroni

Table 2. Proportions of grid cells assigned to eight forest development phase types at a scale of 156.25 m².

Study	Development Phases (% Area)							
	G/R	E	EO	MO	LO	T	D	P
Uholka* (UA)	5.6	7.9	9.4	8.4	30.8	6.1	18.4	13.4
Uholka (UA)	5.6	7.9	9.4	7.7	0	37.7	18.4	13.4
Mirdita (AL)	3.1	0	7.8	19.1	0	47.5	5.6	16.9
Puka (AL)	4.7	1.7	8.2	6.5	0	49.6	2.6	26.7
Rajca (AL)	3.9	4.4	6.5	4.9	0	49.7	7.6	22.9
Havešová (SK)	4.1	6	8.9	4.7	3.8	29.6	15.8	27.1
Kyjov (SK)	9.6	4.6	8.2	4	0	36.6	13.2	23.8

The first row of relative abundance values of development phases for Uholka* (Ukraine, UA) is based on the Modified TC method from the current study, the abundances shown for Uholka (second row), three old-growth European beech forests in Albania (AL; Tabaku 2000) and two in Slovakia (SK; Drößler & Meyer 2006) are based on the original TC (Tabaku 2000) classification protocol with the exception that the Gap and Regeneration phases were summed. G/R, gap/regeneration phase; E, establishment phase; EO, early optimum phase; MO, mid optimum phase; LO, late optimum phase; T, terminal phase; D, decay phase; P, plenter phase.

method was used to correct for multiple mean comparisons (Holm 1979). All computations and the assignment of a development phase for each grid cell were performed in Matlab (v 8.2.0; Mathworks Inc., Natick, MA, US). Statistical analyses were performed in Matlab and SAS (v 9.3; SAS Institute Inc., Cary, NC, US).

Results

Typologies

Table 2 shows the assignments of the typologies resulting from both the TC method (including for sites reported in the literature) and the Modified TC method, reported as a percentage of forest area assigned to each phase. Application of the TC method in the current study resulted in the assignment of the T (37.7%) and P (13.4%) phases to over half of the study area. Taken together, the O phases covered 17.1% of the area, with similar proportions in the EO (9.4%) and MO (7.7%) phases, but no area allocated to the LO phase. The share in the early development phases was 13.5%, with 5.6% in the G/R phase and 7.9% in the E phase. The D phase, slightly more abundant than the combined O phases, comprised an area of 18.4%. Under the Modified TC method, the proportions of the G/R, E, EO, D and P phases remained unchanged. The area allocated to the T phase, however, decreased by 84% (to 6.1%), with some area redirected to the MO phase (which increased to 8.4%) and the rest to the LO phase (30.8%).

Distinctiveness

Some differences among development phases in the five primary attributes of the Modified TC method clearly

reflected the intent and design of the dichotomous rule structure, such as the very low CPA in the G/R phase or the very high NQD in the P phase or the high DS in the D phase (Fig. 3). Similarly, the increasing sequence of MaxD

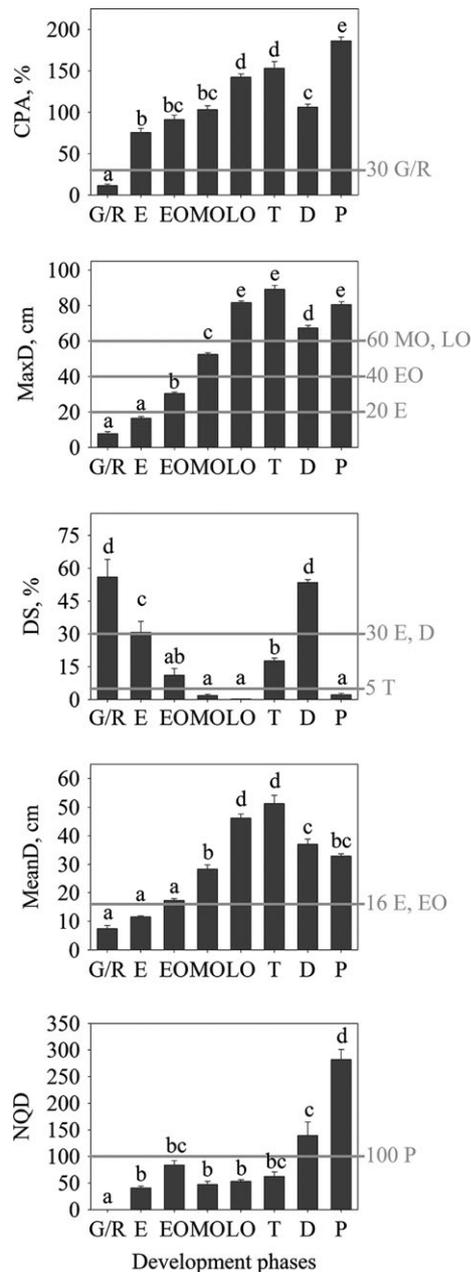


Fig. 3. Mean (\pm SE) values for each primary attribute of the Modified TC method, by development phase type. G/R, gap/regeneration; E, establishment; EO, early optimum; MO, mid optimum; LO, late optimum; T, terminal; D, decay; P, plenter. Horizontal lines indicate the cut-offs for each attribute and the relevant phases. Different letters indicate statistically significant differences between development phases based on permutation tests at the $\alpha = 0.05$ level using the Holm–Bonferroni correction for multiple means comparisons.

from EO to MO to LO reflects the classification rule based on that attribute. However, although only a criterion for the G/R phase, CPA differed significantly among more than half of all phases. Similarly, MeanD was a defining attribute only for the E and EO phases and yet also differed among stages. Average values for CPA, MaxD and MeanD all increased significantly after the G/R, E and EO phases, reached their peak in the T phase (MaxD, MeanD) or the P phase (CPA), and declined in the D phase. The inverse of this pattern was seen for DS, which was lowest in the Optimum phases. By design, NQD values increased from below 100 in the EO, MO, LO and phases to above 100 in the P phase. Average NQD values in the D phase were less than half than in the P phase.

Discussion

Classification protocols are intended to implement the objective assignment of types according to the general requirements of the overarching classification approach (De Cáceres et al. 2015). In the case of development phases delineating portions of the beech forest life cycle, the utility of a classification protocol lies in its ability to differentiate among forest patches dominated by different ecological processes in the kind of old-growth forests from which the life cycle approach was developed (e.g., Leibundgut 1959, 1993; Korpel' 1995). Our examination of the TC method confirmed that the sequence of compound assignment rules was not structured such that all development phases could be assigned as intended, effecting a violation of the prospect requirement. Assignment of the Late Optimum phase should have been readily attainable given that the criterion for diameter at breast height (MaxD) had a threshold of only 60 cm, which is less than half the size that individual beech trees are known to achieve in old-growth forests (Tabaku 2000; Commarmot et al. 2005; Drößler & von Lüpke 2007). Nonetheless, the Late Optimum phase was never assigned because it was impossible to meet this DBH threshold while simultaneously meeting the requirement for the proportion of stand height (<85% PSH). In this Ukrainian old-growth European beech stand, as well as in the Albanian old-growth reserves of Rajca, Mirdita and Puka (Tabaku 2000), the Slovakian reserve of Kyjov (Drößler & Meyer 2006) and at least five other Slovakian old-growth forest reserves (Kucbel et al. 2012), beech trees with a DBH of ≥ 60 cm typically exceed 85% PSH (based on reported stand height curves and heights of the tallest tree in the reserves). Grid cells within these typical old-growth stands would thus be precluded from LO phase assignment and would instead invariably be assigned to the T phase when using the TC method. It is not impossible for local growing conditions to permit individual trees to reach exceptional heights: the tallest beech

trees in the Havešová old-growth reserve in Slovakia reached about 50 m (Drößler & von Lüpke 2007), pushing the 85% PSH threshold just a few cm beyond 60 cm, with the result that 3.8% of grid cells were assigned to the LO phase. However, this extreme exception serves to demonstrate the illogic of an assignment rule requiring two typically mutually exclusive conditions.

This violation of the prospect requirement resulted in a zero probability of being classified into the LO phase and a systematic inflation (positive bias) of the abundance of the T phase. Consequently, when applying the TC method, the current stand in Ukraine demonstrated the same pattern of an absence of the LO phase and dominance by the T phase as has previously been reported in these old-growth beech forest reserves in Albania (Tabaku 2000) and Slovakia (Drößler & Meyer 2006). In all cases, the T phase was the most abundant phase (Albania: 47.5–49.6%; Slovakia: 29.6–36.6%; Ukraine: 37.7%) and the LO phase was entirely (Albania; Slovakia; Ukraine) or nearly absent (Slovakia: 3.8%). Possibly as a consequence of this over-assignment of the T phase, previous applications of the TC method have led to the conclusion that the development cycle is strongly dominated by older phases; in particular, the combination of high relative abundance of the T phase, which comprises 30–50% of the forest area, and the absence or near absence of the LO phase has been branded the signature texture of old-growth beech forests (Tabaku 2000; Drößler & Meyer 2006). However, given the logical sequence of the Optimum phases (Table 1) and our demonstration of the violation of the prospect requirement, we suspect that if the modified TC method (or any other method rectifying this bias) were applied in these Albanian and Slovakian sites, the relative abundance of the T phase would prove notably lower while that of the LO phase would increase commensurately.

We therefore propose a Modified TC method to remedy this bias by omitting the PSH requirement and taking advantage of the DS criterion to distinguish between the LO and T phases instead. Though omitting the PSH criterion admittedly removes the only direct measure of vertical structure from the classification scheme, indirect measures of vertical structure remain *via* the DBH criteria. More importantly, the TC method distinguishes between the LO or T phase entirely using the relation between trees of 60 cm DBH and the height of the largest (tallest) tree in the stand, which has little to do with the ecological process of canopy break-up or gap initiation that marks the end of the LO phase and the inauguration of the T phase: we argue that the distinction between the LO and T phases is primarily a function of differences in mortality processes. It is precisely at the point of transition from the LO to the T phase when processes begin to shift from growth to mortality and eventually regeneration, marking the beginning

of the end of the previous generation and the start of the next in the generational mixture typical of old-growth forest (Meyer 1999; Tabaku 2000; Drößler & Meyer 2006). While mortality should be low in the LO phase, well after the completion of stem exclusion, it should increase in the upper canopy layer with the initiation of the T phase (Korpel' 1995), which is commonly defined as the phase in which tree vitality and the overstorey decline, resulting in increasing mortality of large trees of advanced age and stagnating volume increment with no net accumulation of biomass (Meyer 1999; Tabaku 2000; Drößler & Meyer 2006). It is therefore reasonable to expect that a certain amount of deadwood should be present in the T phase, which is consistent with the generally hypothesized U-shape trajectory of dead woody biomass (Holzwarth et al. 2013).

We therefore determined that a DS threshold value >0% would be consistent with a process definition of the T phase (cf. Meyer 1999; Tabaku 2000; Drößler & Meyer 2006) while still satisfying the prospect requirement. In this study, use of a 5% threshold value for the DS criterion decreased the relative abundance of the T phase by 84%, and commensurately increased the relative abundance of the LO phase from 0 to nearly 31%, without affecting the assignment of most other phases. The exact threshold value within the range of >0–5% DS made only a modest difference in the current study, because the vast majority of grid cells had no deadwood and would remain in the LO phase regardless of the magnitude of any >0% DS threshold value. The relative abundance of the T phase was 11.4% when using >0% and 6.1% when using 5%, and declined even more for all DS thresholds between 5% and 30%. Thus, no matter how low or high the DS threshold above 0%, the relative abundance of the T phase declined substantially compared to the TC method. However, further work is needed to establish the generality of a 5% threshold.

Further refinements

Drößler & Meyer (2006) suggested that calculating CPA based on a single crown layer rather than multiple, overlapping crown layers could alleviate the tendency toward underestimation of the areal proportion in gaps extrapolated from the proportional area assigned to the gap phase. However, this modification actually slightly decreased the relative abundance of the G/R phase because the reduction in the amount of crown area projected outside focal grid cells was less than the addition of crown area from neighbouring trees projected into focal grid cells. Although this method of CPA calculation had little effect, it does have the advantage of better reflecting the light condition of the understorey (cf. Takashima et al. 2006). Nonetheless,

Drößler & Meyer (2006) were correct to point out that the proportion of area in the gap phase is not a measure of the proportion of area in gaps. The difference can be demonstrated by considering the assignment rule for the Gap phase using the TC method, in which a grid cell cannot have a crown projection area of more than 47 m² (<30% CPA at a spatial resolution of 156.25 m²) and hence must have an open gap area of at least 106 m². However, up to 80% of canopy gaps in old-growth beech and beech–fir forests in Central and Southeast Europe are between 40–141 m² (Drößler & von Lüpke 2005; Zeibig et al. 2005; Kenderes et al. 2008; Kuchel et al. 2010). Given that ~13% of sample plot centres in the Uholka old-growth beech reserve are in gaps <50 m² and another ~10% in gaps 51–200 m² (Hobi et al. 2015b), many grid cells containing all or portions of such small gaps would fail to reach the threshold for classification in the gap phase. The majority of small gaps will thus be distributed among grid cells that are allocated to the D and E phases by the TC method, such that the relative abundance of the gap phase will always be much less than the actual proportion of the stand that is in gaps regardless of how CPA is calculated.

Additionally, although not within the scope of the current investigation, it is of note that the spatial scale of the TC method classification approach (i.e. 156.25 m²), although perhaps necessary to capture the gap phase and describe fine-scale forest development phases (Winter & Brambach 2011), is likely suboptimal for monitoring forest stand dynamics and may even incur a bias against the Plenter phase. The primary attribute (NQD) that distinguishes this phase from the Optimum phases requires a minimum of five trees for calculation. At this scale, more than half of all grid cells failed to have a sufficient density of trees to permit calculation, resulting in a default assignment into one of the Optimum phases (i.e. NQD was only able to be calculated in 57% of cells ultimately assigned to the EO phase, 33% for MO and 34% for LO). Because this limitation can be rectified by using larger spatial scales for assessment (e.g., Peck et al. 2015), it represents less a failure of the prospect requirement than a call to consider the applicability of the TC method (original or modified) at the 156.25-m² scale and to reconsider interpretations of stand structure and the abundance of individual development phases when assessed at small scales (cf. Alessandrini et al. 2011; Král et al. 2014b; Zenner et al. 2015a). The minimum appropriate scale for development phase classification is under debate: while the classification typology was originally developed using subjective field assignments of variably-sized phase-patches, some extending up to 2 ha in area (e.g., Korpel' 1995), smaller scales are arguably necessary to capture gap processes (e.g., Hobi et al. 2015b). However, although the advent of rule-based classification protocols may alleviate concerns about the incon-

sistency and subjectivity of development phase assignments (Standovár & Kenderes 2003), it remains to be seen if a given (single) spatial scale is adequate to optimally assign all development phases. Resolution of this issue will require a systematic assessment of the Modified TC method across multiple spatial scales.

Finally, given the requirement for intensive ground-based inventory data, the protocol could likely be made more operational if it were adapted to remotely-sensed data such as LiDAR, which can provide direct measures of both vertical canopy elements and their spatial distribution (Masek et al. 2015). Although recent work has demonstrated the capability of even leaf-off LiDAR to capture some of the primary attributes of the Modified TC method (e.g., crown projection area; Dickinson et al. 2014), further refinement of the protocol could involve adaptation away from ground-based attributes toward remotely-sensed attributes. Further work will be required to demonstrate if, for example, tree diameter cut-offs, which are not currently feasible based on LiDAR data, can be replaced with more readily available attributes, such as the density of canopy layers (cf. Carlton 2016).

Conclusions

While primary attributes and assignment rules have yet to be standardized and a host of different classification protocols exist for assigning forest patches to development phases (e.g., Mayer 1982; Koop 1989; Oldeman 1990; Korpel' 1995; Bobiec et al. 2000; Podlaski 2008; Král et al. 2010, 2014a), our results demonstrate that the design of the classification protocol strongly influences the relative abundances of individual development phases and markedly shapes the interpretation of forest dynamics (Emborg et al. 2000; Tabaku 2000; Drößler & Meyer 2006). Specifically, previous interpretations based on the Tabaku (2000) method that a lack of the late Optimum phase represents a 'signature texture' of old-growth beech forests require reconsideration, perhaps with greater emphasis on the relative abundance of the Terminal, Plenter and Decay phases. To credibly portray forest dynamics, classification protocols must employ consistent rules at all levels of the classification to decompose forest patches into a series of nested types (i.e. phases; cf. Mayr & Bock 2002). Although the assignment of grid cells into all possible types by itself is not yet sufficient proof that the Modified TC method is capable of credibly portraying the shifting mosaic structure that dominates old-growth beech forests, our results do demonstrate that this classification protocol is now capable of meeting the basic prospect requirement for most old-growth European beech forests. However, some limitations persist, leading to a lack of correspondence between the area in the Gap phase and the gap fraction and a poten-

tial underestimation of the Plenter phase at small scales. While the decision on threshold values of the primary attributes used in this, as in all protocols, is arguable, and further work is still required to refine and validate this classification protocol, meeting the prospect requirement clearly is an essential prerequisite for any sensible classification protocol.

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References

- Alessandrini, A., Biondi, F., Di Filippo, A., Ziaco, E. & Piovesan, G. 2011. Tree size distribution at increasing spatial scales converges to the rotated sigmoid curve in two old-growth beech stands of the Italian Apennines. *Forest Ecology and Management* 262: 1950–1962.
- Bobiec, A., van der Burgt, H., Meijer, K., Zuyderduyn, C., Haga, J. & Vlaanderen, B. 2000. Rich deciduous forests in Białowieża as a dynamic mosaic of development phase: premises for nature conservation and restoration management. *Forest Ecology and Management* 130: 159–175.
- Carlton, A.M. 2016. *Using LiDAR to detect the breeding habitat characteristics of the Cerulean warbler (Steophaga cerulea) and identify potential habitat at the landscape level*. M.S. thesis, The Pennsylvania State University, University Park, PA, US.
- Christensen, M., Hahn, K., Mountford, E.P., Ódor, P., Standovár, T., Rozenbergar, D., Diaci, J., Wijdeven, S., Meyer, P., Winter, S. & Vrska, T. 2005. Deadwood in European beech (*Fagus sylvatica*) forest reserves. *Forest Ecology and Management* 210: 267–282.
- Commarmot, B., Bachofen, H., Bundziak, Y., Bürgi, A., Ramp, B., Shparyk, Y., Sukhariuk, D., Viter, R. & Zingg, A. 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. *Forest Snow and Landscape Research* 97: 45–56.
- Commarmot, B., Brändli, U.-B., Hamor, F. & Lavnyy, V. (eds). 2013. *Inventory of the largest virgin beech forest of Europe. A Swiss-Ukrainian scientific adventure*. Swiss Federal Institute of Forest, Snow, and Landscape Research/National Forestry University/Carpathian Biosphere Reserve, Birmensdorf, CH/L'viv, UA/Rakhiv, UA.
- Corona, P., Chirici, G., McRoberts, R.E., Winter, S. & Barbati, A. 2011. Contribution of large-scale forest inventories to biodiversity assessment and monitoring. *Forest Ecology and Management* 262: 2061–2069.
- De Cáceres, M. & Wiser, S.K. 2012. Towards consistency in vegetation classification. *Journal of Vegetation Science* 23: 387–393.
- De Cáceres, M., Chytrý, M., Agrillo, E., Attorre, F., Botta-Dukát, Z., Capelo, J., Czúcz, B., Dengler, J., Ewald, J. (...) & Wiser, S.K. 2015. A comparative framework for broad-scale plot-based vegetation classification. *Applied Vegetation Science* 18: 543–560.
- Dickinson, Y., Zenner, E.K. & Miller, D. 2014. Examining the effect of diverse management strategies on landscape scale patterns of forest structure in Pennsylvania using novel remote sensing techniques. *Canadian Journal of Forest Research* 44: 301–312.
- Drößler, L. & Meyer, P. 2006. Waldentwicklungsphasen in zwei Buchen-Urwaldreservaten in der Slowakei. *Forstarchiv* 77: 155–161.
- Drößler, L. & von Lüpke, B. 2005. Canopy gaps in two virgin beech forest reserves in Slovakia. *Journal of Forest Science* 51: 446–457.
- Drößler, L. & von Lüpke, B. 2007. Bestandesstruktur, Verjüngung und Standortfaktoren in zwei Buchenurwald-Reservaten der Slowakei. *Allgemeine Forst- und Jagdzeitung* 178: 121–135.
- Ellenberg, H. 2009. *Vegetation ecology of Central Europe*, Cambridge University Press, Cambridge, UK.
- Emborg, J., Christensen, M. & Heilmann-Clausen, J. 2000. The structural dynamics of Suserop Skov, a near natural temperate deciduous forest in Denmark. *Forest Ecology and Management* 126: 173–179.
- Good, P.I. 2013. *Permutation tests: a practical guide to resampling methods for testing hypotheses*, 2nd edn. Springer Science & Business Media, Dordrecht, NL.
- Hamor, F. & Brändli, U.-B. 2013. The Uholka-Shyrokyi Luh protected massif – an overview. In: Commarmot, B., Brändli, U.-B., Hamor, F. & Lavnyy, V. (eds). *Inventory of the largest virgin beech forest of Europe. A Swiss-Ukrainian scientific adventure*, pp. 13–17. Swiss Federal Institute of Forest, Snow, and Landscape Research/National Forestry University/Carpathian Biosphere Reserve, Birmensdorf, CH/L'viv, UA/Rakhiv, UA.
- Heurich, M. 2006. *Evaluierung und Entwicklung von Methoden zur automatisierten Erfassung von Waldstrukturen aus Daten flugzeuggetragener Fernerkundungssensoren*. PhD. thesis, Technische Universität München, München, DE.
- Hobi, M.L., Commarmot, B. & Bugmann, H. 2015a. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science* 26: 323–336.
- Hobi, M.L., Ginzler, C., Commarmot, B. & Bugmann, H. 2015b. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. *Ecosphere* 6: 1–15.

- Holeksa, J., Saniga, M., Szwagrzyk, J., Czerniak, M., Staszyńska, K. & Kapusta, P. 2009. A giant tree stand in the West Carpathians – an exception or a relic of formerly widespread mountain European forests? *Forest Ecology and Management* 257: 1577–1585.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6: 65–70.
- Holzwarth, F., Kahl, A., Bauhus, J. & Wirth, C. 2013. Many ways to die – partitioning tree mortality dynamics in a near-natural mixed deciduous forest. *Journal of Ecology* 101: 220–230.
- Huber, M.O. 2011. Statistical models to identify stand development stages by means of stand characteristics. *Canadian Journal of Forest Research* 41: 111–123.
- Kenderes, K., Mihok, B. & Standovár, T. 2008. Thirty years of gap dynamics in a Central European beech forest reserve. *Forestry* 81: 111–123.
- Koop, H. 1989. *Forest dynamics – SILVI-STAR: a comprehensive monitoring system*. Springer, Berlin, DE.
- Korpel', Š. 1995. *Die Urwälder der Westkarpaten*. Gustav Fischer, Stuttgart, DE.
- Král, K., Vrška, T., Hort, L., Adam, D. & Šamonil, P. 2010. Development phases in a temperate natural spruce–fir–beech forest: determination by a supervised classification method. *European Journal of Forest Research* 129: 339–351.
- Král, K., McMahan, S.M., Janík, D., Dušan, A. & Vrška, T. 2014a. Patch mosaic of developmental stages in central European natural forests along an elevation and vegetation gradient. *Forest Ecology and Management* 330: 17–28.
- Král, K., Valtera, M., Janík, D., Šamonil, P. & Vrška, T. 2014b. Spatial variability of general stand characteristics in central European beech-dominated natural stands – effects of scale. *Forest Ecology and Management* 328: 353–364.
- Kucbel, S., Jaloviar, P., Saniga, M., Vencurik, J. & Klimaš, V. 2010. Canopy gaps in an old-growth fir–beech forest remnant of Western Carpathians. *European Journal of Forest Research* 129: 249–259.
- Kucbel, S., Saniga, M., Jaloviar, P. & Vencurik, J. 2012. Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: a 40-year perspective. *Forest Ecology and Management* 264: 125–133.
- Leibundgut, H. 1959. Über Zweck und Methodik der Struktur- und Zuwachsanalyse von Urwäldern. *Schweizerische Zeitschrift für Forstwesen* 110: 111–124.
- Leibundgut, H. 1978. Über die Dynamik europäischer Urwälder. *Allgemeine Forst Zeitschrift* 33: 686–690.
- Leibundgut, H. 1993. *Europäische Urwälder*. Paul Haupt, Bern, CH.
- Masek, J.G., Hayes, D.J., Hughes, M.J., Healey, S.P. & Turner, D.P. 2015. The role of remote sensing in process-scaling studies of managed forest ecosystems. *Forest Ecology and Management* 355: 109–123.
- Mayer, H.A. 1982. *Waldbau auf soziologisch-ökologischer Grundlage*, 3rd edn. Gustav Fischer, Stuttgart, DE.
- Mayr, E. & Bock, W.J. 2002. Classifications and other ordering systems. *Journal of Zoological Systematics and Evolutionary Research* 40: 169–194.
- Meyer, H.A. 1952. Structure, growth, and drain in balanced uneven-aged forests. *Journal of Forestry* 50: 85–92.
- Meyer, P. 1999. Bestimmung der Waldentwicklungsphasen und der Texturdiversität in Naturwäldern. *Allgemeine Forst- und Jagdzeitung* 170: 203–211.
- Michailoff, I. 1943. Zahlenmässiges Verfahren für die Ausführung der Bestandeshöhenkurven. *Forstwiss. Forstwissenschaftliches Centralblatt und Tharandter Forstliches Jahrbuch* 6: 273–279.
- Oldeman, R.A. 1990. *Forests: elements of silvology*. Springer, Berlin, DE.
- Peck, J.E., Zenner, E.K., Hobi, M.L. & Commarmot, B. 2015. Should reference conditions be drawn from a single 10 ha plot? Assessing representativeness in a 10,000 ha old-growth European beech forest? *Restoration Ecology* 23: 927–935.
- Podlaski, R. 2008. Dynamics in Central European near-natural Abies-Fagus forests: does the mosaic-cycle approach provide an appropriate model? *Journal of Vegetation Science* 19: 173–182.
- Pressey, R.L. 2004. Conservation planning and biodiversity: assembling the best data for the job. *Conservation Biology* 18: 1677–1681.
- Pruša, E. 1985. *Die Böhmisches und Mährischen Urwälder – ihre Struktur und Ökologie*. Akademia Verlag der Tschechoslowakischen Akademie der Wissenschaften, Prague, CZ.
- Rall, H. 1990. Waldinventur und Waldpflegeplanung im Nationalpark Berchtesgaden 1983–1986. In: Kral, F. & Rall, H. (eds.). *Wälder, Geschichte, Zustand, Planung. Forschungsbericht 20*, pp. 21–87. Berchtesgaden Nationalpark, Berchtesgaden, DE.
- Schütz, J.-Ph. 2001. *Der Plenterwald und weitere Formen strukturierter und gemischter Wälder*. Parey Buchverlag, Berlin, DE.
- Standovár, T. & Kenderes, K. 2003. A review on natural stand dynamics in beechwoods of East Central Europe. *Applied Ecology and Environmental Research* 1: 19–46.
- Tabaku, V. 2000. *Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und Wirtschaftswäldern*. PhD Thesis, Universität Göttingen, Cuvillier, Göttingen, DE.
- Takashima, A., Kume, A. & Yoshida, S. 2006. Methods for estimating understory light conditions using crown projection maps and topographic data. *Ecological Research* 21: 560–569.
- Watt, A.S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35: 1–22.
- Westphal, C., Tremer, N., von Oheimb, G., Hansen, J., von Gadow, K. & Härdtle, W. 2006. Is the reverse J-shaped diameter distribution universally applicable in European virgin beech forests? *Forest Ecology and Management* 223: 75–83.
- Winter, S. & Brambach, F. 2011. Determination of a common forest life cycle assessment method for biodiversity evaluation. *Forest Ecology and Management* 262: 2120–2132.

- Zeibig, A., Diaci, J. & Wagner, S. 2005. Gap disturbance patterns of a *Fagus sylvatica* virgin forest remnant in the mountain vegetation belt of Slovenia. *Forest Snow and Landscape Research* 79: 69–80.
- Zenner, E.K., Peck, J.E., Hobi, M.L. & Commarmot, B. 2015a. The dynamics of structure across a primeval European beech stand. *Forestry* 88: 180–189.
- Zenner, E.K., Sagheb-Talebi, K., Akhavan, R. & Peck, J.E. 2015b. Integration of small-scale canopy dynamics smoothes live-tree structural complexity across development stages in old-growth Oriental beech (*Fagus orientalis* Lipsky) forests at the multi-gap scale. *Forest Ecology and Management* 335: 26–36.