

Stand inventory data from the 10 ha forest research plot in Uholka: 15 years of primeval beech forest development

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Metadata

Introduction

Primeval forests in Europe are extremely scarce since deforestation for cultivation of crops and pasture was already extensive around 1000 BC (Kaplan et al. 2009). Today, remnants of primeval forests mainly occur in eastern and northern Europe (Sabatini et al. 2018).

European beech forests, which form one of the most common forest types in Europe being frequent from southern Italy to southern Scandinavia and from northern Spain to the Carpathians (San Miguel Ayanz et al. 2016), have been particularly altered by humans (Hannah et al. 1995).

As the recovery of primeval forest features and natural processes in forest ecosystems requires a long time (Paillet et al. 2015), primeval forests are of particular interest for studying natural processes and the distinctive features of unmanaged forests. This led to the establishment of long-term monitoring plots of various sizes (0.1 ha - several ha) in several parts of Europe already during the 1950's, mostly following a protocol developed by Leibundgut (1959).

Since, the development of primeval, old-growth and unmanaged beech forests has been explored in numerous studies, e.g., focusing on structural dynamics (e.g., Emborg et al. 2000, von Oheimb et al. 2005), the influence of former management (Heiri et al. 2009), the comparison of managed and primeval beech forests (Commarmot et al. 2005) or the disturbance regime of primeval beech forests (Trotsiuk et al. 2012). Due to the decrease of relative border length with increasing plot area and the associated decrease of edge effects, large forest plots are suited to determine spatial patterns in species association (e.g, Wiegand et al. 2007) or in the aggregation of large trees (Lutz et al. 2013).

Here, we present a forest inventory dataset from a permanent plot of 10 ha in the Uholka part of the Uholka-Shyrokyi Luh forest where all trees above a DBH ≥ 6 cm have been measured during 4 inventories. The area harbors one of the largest remnants of primeval forest of European beech and is part of the Carpathian Biosphere Reserve (CBR) in Transcarpathia, Ukraine, and the UNESCO World Heritage 'Ancient and Primeval Beech Forests of the Carpathians and Other Regions of Europe'. The plot has been established in 2000 and remeasured in 2005, 2010 and 2015.

To allow accounting for topographic heterogeneity within the plot, we include a Digital Elevation Model (DEM) with a resolution of 2 x 2 m. The DEM was derived from an Airborne Laser Scan acquired in May 2018.

The dataset is especially valuable for comparison when used with datasets from similar forest plots. Differences between the dataset presented here and other datasets mostly

refer to differences in calliper thresholds and plot size. Whereas all trees above a DBH ≥ 1 cm are being measured in the CTFS-ForestGEO network (Anderson-Teixeira et al. 2015), on ICP-Forests plots trees above a DBH ≥ 5 cm are included during inventories (Dobbertin and Neumann 2016). Whilst the minimum area for a ICP-Forests plot of level II is 0.25 ha (Dobbertin and Neumann 2016), the median size of the 59 plots included in the CTFS-ForestGEO network is 25 ha, ranging between 4 and 60 ha (Anderson-Teixeira et al. 2015).

Class I. Data Set Descriptors

A. Data set identity:

Forest inventory data from a 10 hectare stem mapped plot in the primeval beech forest of Uholka-Shyrokyi Luh.

B. Data set identifier:

N/A

C. Data description:

The dataset consists of four inventories carried out on a 10 ha permanent plot in the Uholka part of the Uholka-Shyrokyi Luh primeval beech forest in Transcarpathia, Ukraine (Figure 1). The plot was established in 2000, all living and dead trees with a Diameter at Breast Height (DBH) ≥ 60 mm were identified to species, two DBH per tree were measured crosswise and the status (alive/dead) and the canopy layer of the trees were assessed. The canopy layer was assessed in three classes (tree height $< 1/3$, tree height $1/3 - 2/3$ and tree height $> 2/3$ of top height of the stand). On a subset of the trees, total height and diameter at 7 m height (D_7) were measured to allow volume calculations. The trees were revisited and measured in 2005, 2010 and 2015. The tree measurements were performed after completion of the growing season, i.e., the inventory in 2015 was done after August 2015 and before onset of the following growing season in Mai 2016. Trees were identified based on the stem-tags and their mapped position. They include new recruits (ingrowth), i.e. trees that have grown over the caliper threshold of 60 mm in the 2nd, 3rd or 4th inventory since the last inventory. In total, 4820 individual trees were measured including 14050 individual observations throughout all inventories.

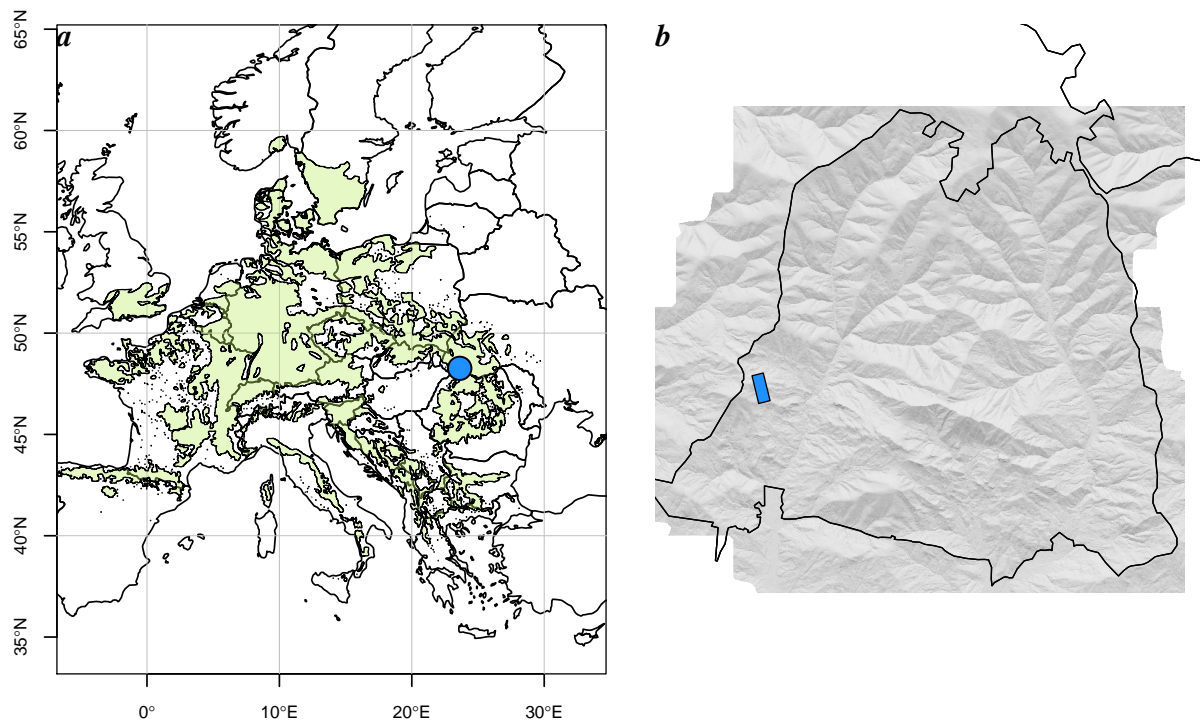


Figure 1: Position of the Uholka-Shyrokyi Luh forest within Europe in relation to the natural distribution of beech according to EUFORGEN (2009) (a) and the location of the plot within the Uholka massif (b)

1. Originators:

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Class II. Research Origin Descriptors

A. Overall project description

1. Project title: Primeval forest structures and biodiversity: A Swiss-Ukrainian research cooperation

2. Originators:

PI's of the overall project:

1999-2016: Brigitte Commarmot, Swiss Federal Research Institute for Forest, Snow and Landscape Research WSL, Forest Resources and Management, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.

2017-2020: Peter Brang, Swiss Federal Research Institute for Forest, Snow and Landscape Research WSL, Forest Resources and Management, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.

3. Period of study:

Since 1999, ongoing.

4. Objectives of overall project:

Since 1999, the Swiss Federal Research Institute WSL cooperates with institutions in Ukraine. The objectives of the project are:

- to promote the primeval beech forest Uholka-Shyrokyi Luh as hotspot of scientific exchange across borders and disciplines
- to promote young scientists
- to create synergies across projects

5. Abstract of overall project

Since 1999, the Swiss Federal Research Institute WSL cooperates with several research and conservation institutions in Ukraine. The project includes a wide range of activities and is highly interdisciplinary, bringing together experts from several fields such as forestry, forest ecology, biodiversity, energy change and remote sensing. In the following, the key subprojects are outlined.

Projects focusing on forest ecology: Studying primeval forests was one of the key foci of the cooperation. This led to the establishment of a 10 ha plot in the primeval beech forest of Uholka in cooperation with the Carpathian Biosphere Reserve (CBR), Rakhiv, and the Vasyl-Stefaniuk Precarpathian University, Ivano-Frankivsk in 2000 (Commarmot et al. 2005). The data provide detailed information on demographic rates as well as spatial patterns and processes and have since been used in numerous publications, e.g., on developmental phases in primeval beech forests (Zenner et al. 2015) or mortality of European beech (Hülsmann et al. 2016).

In 2010, a large scale sample plot inventory was carried out to characterize the composition and structure of the entire Uholka-Shyrokyi Luh massif (Commarmot et al. 2013). This data was used to assess the gap structure of primeval beech forests (Hobi et al. 2015*b*) and to describe patterns and processes in primeval beech forests (Hobi et al. 2015*a*). A large part of the sample plots will be remeasured in 2019.

In an additional study in the Uholka massif which started in 2017, above- and belowground growth and physiological traits of seedlings and saplings as well as adult tree fecundity are studied to elucidate the processes leading to beech dominance. The three species studied are beech, *Acer platanoides* and *Acer pseudoplatanus*.

To elucidate the age structure using dendrochronological analyses, four permanent plots of 1000 m² each have been established in 2010 close to the 10 ha permanent plot (Trotsiuk et al. 2012). Within these plots, increment cores were taken from all living trees with DBH \geq 6 cm.

Two remote sensing datasets were gathered in 2017 and 2018 to allow further analysis concerning the spatial variation of disturbances of various levels. In summer 2017, stereo-photo imagery of the Uholka-Shyrokyi Luh massif was captured, and in spring 2018, during leave-off conditions, airborne laser scan data was gathered.

In addition, six permanent plots of 0.5 ha were established in primeval forests in 2018 to better understand the dynamics of spruce-dominated primeval forests close to the upper tree line in the Chornohora range.

Other projects: The primeval beech forests of Transcarpathia are not only key to investigate hypotheses related to forest ecology but also as a hotspot of biodiversity. During the sample plot inventory in 2010, epiphytic lichens were collected on the sample plots to study their requirements regarding forest structure and composition (Dymytrova et al. 2014). Additionally, saproxylic beetles that often depend on beech forests (Müller et al. 2013) were collected at 20 sites in the Uholka massif between 2010 and 2013 to determine the influence of canopy gaps on saproxylic beetles (Lachat et al. 2016). In 2017 and 2018, a more detailed

monitoring of saproxylic beetles and fungi was established on the 10 ha plot with a reference plot in a managed forest nearby.

To understand the distribution and frequency of different *Armillaria* species within the primeval forests of Uholka-Shyrokyi Luh and the Chornohora range, a sampling on a regular 1.5 x 1.5 km grid (resulting in 52 plots in the Uholka-Shyrokyi Luh forest) was carried out (Tsykun et al. 2012).

The Ukrainian Carpathians are not only covered by primeval forests - a majority of the forests are heavily influenced by humans and have mainly been transformed to secondary spruce forests. Often, these forests are poorly adapted to the site conditions and therefore vulnerable to bark beetle (*Ips typographus*) attacks (Seidl et al. 2007). Moreover, compared to primary stands, these secondary stands are more sensitive to drought (e.g., van der Maaten-Theunissen et al. (2013)). To provide guidelines how these forests could be transformed into more stable, mixed, and structurally diverse forests, an experiment has been established in 2006 at a site close to Rakhiv. The experiment follows a block design with replication and four treatments, i.e. three different degrees of removal and a control plot. The trees and regeneration layers on the 12 plots have since been remeasured in 2012 and 2018.

Timber from the Carpathian forests plays an important role for the local heat supply of the region. Using wood also as a source for energy is investigated at eight research sites in three oblasts (administrative regions) since 2017. With this in-depth research, this subproject aims at supporting Ukraine's green energy transition with valuable data.

6. Sources of funding

1999: Commission des relations internationales du CEPF

2002-2003: Swiss National Science Foundation SNF, SCOPES Program 7IP062590

2005-2008: Swiss National Science Foundation SNF, SCOPES Program IIB74A0-111087

2008-2012: Swiss State Secretariat for Education, Research and Innovation (SERI)

2013: Swiss federal research institute WSL, Internal project

2017-2020: Swiss State Secretariat for Education, Research and Innovation (SERI)

B. Specific subproject description

B1, Site description:

The permanent plot is located in an old-growth stand, covers an area of 10 ha and is situated at 48.2695°N, 23.6207°E at an altitude of 700-800 m a.s.l. The plot is mainly south-east exposed on slopes with a grade between 20 and 40 %. Soils mainly consist of dystric cambisols (Commarmot et al. 2005). Mean annual temperature is 7°C with a mean temperature of -4°C in January and 17°C in July (Brändli and Dowhanytsch 2003). Mean annual precipitation is 950 mm. The plot is dominated by European beech that made up around 95% of the BA in 2015.

Since it's establishment in 2000, two major disturbance events affecting the plot occurred: In April 2007, a regional storm damaged and toppled single trees. In October 2009, heavy wet snowfall lasting 4 days damaged particularly thin trees (Shparyk et al. 2018). These disturbances led to a decrease in BA of living trees in 2010 of about -1.7 m² ha⁻¹ to 37.5 m²ha⁻¹, and, as a legacy effect to an increase in the number of stems of + 120 trees per ha to 414 trees per ha in 2015. The increase in number of stems was mainly driven by light-demanding species such as *Acer sp.*.

B2, Experimental design:

The permanent plot was chosen subjectively in 2000. The selection was based on *a)* relative homogeneity of the plot with regard to forest structure, *b)* accessibility of the plot from the next village, *c)* the inclusion of the entire plot in the core zone of the reserve. The plot covers an area of 99998 m² and is not representative for the Uholka-Shyrokyi Luh forest. Compared to the data from the sample plot inventory (Commarmot et al. 2013), BA and number of large stems (DBH ≥ 80 cm) was higher whilst the number of stems per hectare was lower on the research plot in 2010 (Peck et al. 2015).

B3, Research methods:

The permanent plot was divided into 40 square subplots of $\approx 2500 \text{ m}^2$ (50x50 m) to facilitate the measurements. In 2000, all dead and living trees with DBH ≥ 60 mm were identified to species level if possible and two stem diameters (D1 and D2) were measured crosswise at an accuracy of one millimetre. On each subplot, at least 10 trees covering the whole DBH distribution were randomly chosen as tariff trees. On these trees and on all dead standing and broken trees (stumps), total height was measured for volume calculations. On tariff trees, additional measurements included Diameter at 7 m (D₇) and the height of the beginning of

the crown. Crown height was defined as the point where the first branch belonging to the crown, excluding epicormic branches, branches of the stem.

During the subsequent inventories in 2005, 2010 and 2015, all living and dead trees that were measured at least in one of the previous inventories were remeasured, and trees that had recently exceeded a DBH of 60 mm (ingrowth) were added to the inventory.

DBH was measured using a calliper with a maximum range of 80 cm (2000 and 2015) or a maximum range of 100 cm (2005, 2010), respectively. A dbh-measurement tape for trees with a DBH ≥ 80 cm or ≥ 100 cm was used. Total height and crown length was measured using a Vertex III device (Haglof Sweden AB) and a pole calliper was used for measurements of D7. The manual used for the latest inventory can be found in the supplementary material S2.

All trees were stem tagged and mapped in a 'local' coordinate system. During the inventory in 2015, all vertices of the subplots were measured using a TrimbleTMGeoXH (Trimble Inc., Sunnyvale CA, USA) device. The raw data (.ssh) was postprocessed using the Trimble Pathfinder OfficeTMsoftware. Based on these measurements, all trees were georeferenced to UTM 34N using the vec2dtransf-package (Carrillo 2014) in the statistical software R (R Core Team 2017).

In May 2018 an Airborne Laser Scan (ALS) was flown using an Optech ALTM Gemini (Optech Inc., Canada) by Aviation Accounting Center LLC, Kyiv, Ukraine, covering the Uholka and Shyrokyi Luh massif with a mean pulse density of 19.2 returns per m². A DEM was derived from the raw data using lastools (Isenburg 2014).

B 4, Project personnel:

Brigitte Commarmot was the PI between 2000 and 2017. Yuriy Shparyk led the field work between 2000 and 2010 and co-led the field work with Jonas Stillhard in 2015. Roman Bidychak, Roman Falko, Mirosław Kabal, Jens Nitzsche, Gilbert Projer, Viktor Shparyk, Dmytro Sukhariuk, Roman Viter, and Jonas Wicky carried out field work in different years. Martina Hobi validated the dataset in 2010; Jonas Stillhard and Lisa Hülsmann validated the dataset in 2016. The georeferencing of all data has been carried out by Jens Nitzsche and Jonas Stillhard. Christian Ginzler calculated the DEM from the raw ALS-data.

Class III. Data set status and accessibility

A. Status

Latest update: The dataset was last updated 4/30/2016

Latest archive date: The dataset was last archived 1/31/2017

Metadata status: Metadata was updated prior to publication.

Data verification: In 2016, the dataset was validated in several steps. On all trees, the status development (i.e., alive-dead) and species assignment were checked. If a tree was not measured during an inventory but found again during a subsequent one, an entry for the missing inventory, containing information on species and status (if applicable) was generated. DBH, total height and D7 development were not validated nor changed to give analysts the freedom to decide themselves how to handle implausible and/or missing entries. On 264 trees, heights were measured in 2005 and 2010, although the trees were broken (stem/crown breakage). These values were removed during data validation. All trees with a mean diameter < 60 mm were removed during data validation. To facilitate the use of the data for potential users, we restructured the dataset and removed qualitatively assessed values.

As the differences in calliper ranges between the inventories might have an effect on DBH increment, we checked for differences in DBH increment and DBH development between the inventory periods. We did not find a systematic error associated with the change of the measuring method between the inventories.

B. Accessibility

Storage location: All data is available as supporting information DataS1.zip to this publication. An original copy of the dataset is stored on a server of the Swiss Federal Research Institute WSL, Birmensdorf, Switzerland.

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Copyright restrictions: No copyright restrictions.

Proprietary restrictions: No proprietary restrictions. When making use of the dataset this paper has to be cited.

Costs: None

Class IV. Data set description

A. Data Set File

1. uholka_trees.csv

1.2 Size: 17 columns and 14116 rows (not including header row), 2155 kb.

1.3 Format and storage mode: Comma-separated values (.csv).

1.4 Header information: Header describes the content of each column as described in table 1.

1.5 Alphanumeric attributes: Mixed

1.6 Authentication procedure: The file contains 17 columns and 14116 rows (not including the header row). The sum of dbh_1 is 4002594 and htot contains 12638 NA-values.

2. uholka_points.csv

2.1 Size: 5 columns and 55 rows (not including header row), 4 kb.

2.2 Format and storage mode: Comma-separated values (.csv).

2.3 Header information: Header describes the content of each column as described in table 2.

2.4 Alphanumeric attributes: Mixed

2.5 Authentication procedure: The file contains 5 columns and 55 rows (not including the header row). The sum of point_nr is 1540.

3. uholka_dem_2017_utm34N.tiff

3.1 Size: 385 kb.

3.2 Format and storage mode: GeoTiff (.tiff).

3.3 Header information: No header information available.

3.4 Alphanumeric attributes: Numeric

3.5 Authentication procedure: The minimum value of the cells is 699.677, the maximum value is 788.243.

B. Variable Information

Table 1: Variables contained in file uholka_trees.csv

Variable Name	Definition/Description	Data Format	Unit
tree_nr	Number of the tree, unique identifier for the tree	Integer	
year	Year of measurement, together with tree_nr unique identifier for observation	Integer	
species_code	Species code (see table 3 for encoding)	Integer	
species	Scientific name of species	character	
status_1	Tree found (1) or not found (0) during inventory	Boolean	
status_2	Tree alive (1) or dead (0)	Boolean	
status_3	Tree standing (1) or lying (0)	Boolean	
status_4	Only for dead trees: entire tree (1) or broken tree (snag), (0)	Boolean	
dbh_1	Diameter at Breast Height (DBH) 1, D1	Integer	<i>mm</i>
dbh_2	Diameter at Breast Height (DBH) 2, D2	Integer	<i>mm</i>
height	Total height of the tree, measured only on a subset of trees	Float	<i>m</i>
height_crown	Height of the beginning of crown, measured only on a subset of trees	Float	<i>m</i>
d_7	Diameter at 7 m (D7), measured only on a subset of trees	Integer	<i>cm</i>
x_local	X -coordinates in local reference system	Float	<i>m</i>
y_local	Y -coordinates in local reference system	Float	<i>m</i>
x_utm34n	X -coordinates in projected reference system (UTM 34 N)	Float	
y_utm34n	Y -coordinates in projected reference system (UTM 34 N)	Float	

Table 2: Variables contained in file uholka_points.csv

Variable Name	Definition/Description	Data Format	Unit
point_nr	Number of vertex	Integer	
x_local	X -coordinates in local reference system	Float	<i>m</i>
y_local	Y -coordinates in local reference system	Float	<i>m</i>
x_utm34n	X -coordinates in projected reference system (UTM 34 N)	Float	
y_utm34n	Y -coordinates in projected reference system (UTM 34 N)	Float	

Table 3: Species Codes

Code	Latin	English
411	<i>Fagus sylvatica</i> L.	European Beech
431	<i>Fraxinus excelsior</i> L.	European Ash
441	<i>Acer pseudoplatanus</i> L.	Sycamore
442	<i>Acer platanoides</i> L.	Norway Maple
511	<i>Ulmus glabra</i> Huds.	Scotch Elm
521	<i>Prunus avium</i> L.	Wild Cherry
534	<i>Salix caprea</i> L.	Goat Willow
551	<i>Sorbus aria</i> (L.) Crantz	Beam Tree
552	<i>Sorbus aucuparia</i> L.	Rowan

Class V. Supplemental Descriptors

A. Data Aquisition

A 1, Data Forms

During the inventories in 2000, 2005 and 2010, all data was gathered on paper forms. This data has subsequently been digitized and the forms have been scanned. The scans are stored on a server at WSL. In 2015, data has been collected using StandInv, a data collection software developed at WSL. The original StandInv-files are stored on a server at WSL.

B. Quality assurance procedures

The digitized datasets (inventories 2000, 2005 and 2010) have been checked for outliers and implausible entries. Such values have been double checked in the original field forms.

C. Publications

The following publications made use of the dataset:

Commarmot, B., H. Bachofen, Y. Bundziak, A. Bürgi, B. Ramp, Y. Shparyk, D. Sukhariuk, R. Viter, and A. Zingg. 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. *Forest Snow and Landscape Research* **79**:45–56

Zenner, E. K., J. E. Peck, M. L. Hobi, and B. Commarmot. 2015. The dynamics of structure

across scale in a primaeval European beech stand. *Forestry* **88**:180–189

Peck, J. E., B. Commarmot, M. L. Hobi, and E. K. Zenner. 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

Hülsmann, L., H. Bugmann, B. Commarmot, P. Meyer, S. Zimmermann, and P. Brang. 2016. Does one model fit all? Patterns of beech mortality in natural forests of three European regions. *Ecological Applications* **26**:2465–2479

Zenner, E. K., J. E. Peck, M. L. Hobi, and B. Commarmot. 2016. Validation of a classification protocol: meeting the prospect requirement and ensuring distinctiveness when assigning forest development phases. *Applied Vegetation Science* **19**:541–552

The plot has been a reference site for comparison of stand characteristics derived from Terrestrial Laser Scan data with managed forests by:

Willim, K., M. Stiers, P. Annighöfer, C. Ammer, M. Ehbrecht, M. Kabal, J. Stillhard, and D. Seidel. 2019. Assessing Understory Complexity in Beech-dominated Forests (*Fagus sylvatica* L.) in Central Europe—From Managed to Primary Forests. *Sensors* **19**:1684

Stiers, M., K. Willim, D. Seidel, M. Ehbrecht, M. Kabal, C. Ammer, and P. Annighöfer. 2018. A quantitative comparison of the structural complexity of managed, lately unmanaged and primary European beech (*Fagus sylvatica* L.) forests. *Forest Ecology and Management* **430**:357–365

Acknowledgments

These measurements would not have been possible without the support of Fedir Hamor, Mykola Rybak and local staff of CBR, especially Vasyl Rehush. We are grateful for the ongoing support of WSL.

We thank the two anonymous reviewers for their valuable comments which considerably improved the manuscript.

References

- Anderson-Teixeira, K. J., S. J. Davies, A. C. Bennett, E. B. Gonzalez-Akre, H. C. Muller-Landau, S. Joseph Wright, K. Abu Salim, A. M. Almeyda Zambrano, A. Alonso, J. L. Baltzer, Y. Basset, N. A. Bourg, E. N. Broadbent, W. Y. Brockelman, S. Bunyavejchewin, D. F. R. P. Burslem, N. Butt, M. Cao, D. Cardenas, G. B. Chuyong, K. Clay, S. Cordell, H. S. Dattaraja, X. Deng, M. Detto, X. Du, A. Duque, D. L. Erikson, C. E. Ewango, G. A. Fischer, C. Fletcher, R. B. Foster, C. P. Giardina, G. S. Gilbert, N. Gunatilleke, S. Gunatilleke, Z. Hao, W. W. Hargrove, T. B. Hart, B. C. Hau, F. He, F. M. Hoffman, R. W. Howe, S. P. Hubbell, F. M. Inman-Narahari, P. A. Jansen, M. Jiang, D. J. Johnson, M. Kanzaki, A. R. Kassim, D. Kenfack, S. Kibet, M. F. Kinnaird, L. Korte, K. Kral, J. Kumar, A. J. Larson, Y. Li, X. Li, S. Liu, S. K. Lum, J. A. Lutz, K. Ma, D. M. Maddalena, J.-R. Makana, Y. Malhi, T. Marthews, R. Mat Serudin, S. M. McMahon, W. J. McShea, H. R. Memiaghe, X. Mi, T. Mizuno, M. Morecroft, J. A. Myers, V. Novotny, A. A. de Oliveira, P. S. Ong, D. A. Orwig, R. Ostertag, J. den Ouden, G. G. Parker, R. P. Phillips, L. Sack, M. N. Sainge, W. Sang, K. Sri-ngernyuang, R. Sukumar, I.-F. Sun, W. Sungpalee, H. S. Suresh, S. Tan, S. C. Thomas, D. W. Thomas, J. Thompson, B. L. Turner, M. Uriarte, R. Valencia, M. I. Vallejo, A. Vicentini, T. Vrška, X. Wang, X. Wang, G. Weiblen, A. Wolf, H. Xu, S. Yap, and J. Zimmerman. 2015. CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology* **21**:528–549.
- Brändli, U.-B., and J. Dowhanytsch. 2003. *Urwälder im Zentrum Europas. Ein Naturführer durch das Karpaten-Biosphärenreservat in der Ukraine*. Eidgenössische Forschungsanstalt WSL, Karpaten-Biosphärenreservat, Rachiw, Haupt Verlag Bern.
- Carrillo, G., 2014. `vec2dtransf`: 2D Cartesian Coordinate Transformation. URL <https://CRAN.R-project.org/package=vec2dtransf>.
- Commarmot, B., H. Bachofen, Y. Bundziak, A. Bürgi, B. Ramp, Y. Shparyk, D. Sukhariuk, R. Viter, and A. Zingg. 2005. Structures of virgin and managed beech forests in Uholka (Ukraine) and Sihlwald (Switzerland): a comparative study. *Forest Snow and Landscape Research* **79**:45–56.
- Commarmot, B., U.-B. Brändli, F. Hamor, and V. Lavnyy, editors. 2013. *Inventory of the largest primeval beech forest in Europe: A Swiss-Ukrainian scientific adventure*. Swiss Federal Inst. for Forest, Snow and Landscape Research.
- Dobbertin, M., and M. Neumann, 2016. Part V: Tree Growth., Page 17 . Thünen Institute of

- Forest Ecosystems, Eberswalde, Germany. URL <http://www.icp-forests.org/manual.htm>.
- Dymytrova, L., O. Nadyeina, M. L. Hobi, and C. Scheidegger. 2014. Topographic and forest-stand variables determining epiphytic lichen diversity in the primeval beech forest in the Ukrainian Carpathians. *Biodiversity and Conservation* **23**:1367–1394. URL <https://doi.org/10.1007/s10531-014-0670-1>.
- Emborg, J., M. Christensen, and J. Heilmann-Clausen. 2000. The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management* **126**:173–189.
- EUFORGEN. 2009. Distribution map of Beech (*Fagus sylvatica*). www.euforgen.de.
- Hannah, L., J. L. Carr, and A. Lankerani. 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. *Biodiversity & Conservation* **4**:128–155.
- Heiri, C., A. Wolf, L. Rohrer, and H. Bugmann. 2009. Forty years of natural dynamics in Swiss beech forests: structure, composition, and the influence of former management. *Ecological Applications* **19**:1920–1934.
- Hobi, M. L., B. Commarmot, and H. Bugmann. 2015*a*. Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal of Vegetation Science* **26**:323–336.
- Hobi, M. L., C. Ginzler, B. Commarmot, and H. Bugmann. 2015*b*. Gap pattern of the largest primeval beech forest of Europe revealed by remote sensing. *Ecosphere* **6**:1–15.
- Hülsmann, L., H. Bugmann, B. Commarmot, P. Meyer, S. Zimmermann, and P. Brang. 2016. Does one model fit all? Patterns of beech mortality in natural forests of three European regions. *Ecological Applications* **26**:2465–2479.
- Isenburg, M. 2014. LAStools—Efficient LiDAR Processing Software. Available online: lastools.org.
- Kaplan, J. O., K. M. Krumhardt, and N. Zimmermann. 2009. The prehistoric and preindustrial deforestation of Europe. *Quaternary Science Reviews* **28**:3016–3034.
- Lachat, T., M. Chumak, V. Chumak, O. Jakoby, J. Müller, M. Tanadini, and B. Wermelinger. 2016. Influence of canopy gaps on saproxylic beetles in primeval beech forests: a case study from the Uholka-Shyrokyi Luh forest, Ukraine. *Insect Conservation and Diversity* **9**:559–573.

- Leibundgut, H. 1959. Über Zweck und Methodik der Struktur-und Zuwachsanalyse von Urwäldern. *Schweizerische Zeitschrift für Forstwesen* **110**:111–124.
- Lutz, J. A., A. J. Larson, J. A. Freund, M. E. Swanson, and K. J. Bible. 2013. The importance of large-diameter trees to forest structural heterogeneity. *PLoS One* **8**:e82784.
- Müller, J., J. Brunet, A. Brin, C. Bouget, H. Brustel, H. Bussler, B. Foerster, G. Isacsson, F. Koehler, T. Lachat, and M. M. Gossner. 2013. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. *Insect Conservation and Diversity* **6**:162–169.
- Paillet, Y., C. Pernot, V. Boulanger, N. Debaive, M. Fuhr, O. Gilg, and F. Gosselin. 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. *Forest Ecology and Management* **346**:51–64.
- Peck, J. E., B. Commarmot, M. L. Hobi, and E. K. Zenner. 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.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Sabatini, F. M., S. Burrascano, W. S. Keeton, C. Levers, M. Lindner, F. Pötzschner, P. J. Verkerk, J. Bauhus, E. Buchwald, O. Chaskovsky, N. Debaive, F. Horváth, M. Garbarino, N. Grigoriadis, F. Lombardi, I. Marques Duarte, P. Meyer, R. Midteng, S. Mikac, M. Mikoláš, R. Motta, G. Mozgeris, L. Nunes, M. Panayotov, P. Ódor, A. Ruete, B. Simovski, J. Stillhard, M. Svoboda, J. Szwagrzyk, O.-P. Tikkanen, R. Volosyanchuk, T. Vrska, T. Zlatanov, and T. Kuemmerle. 2018. Where are Europe’s last primary forests? *Diversity and Distributions* **24**:1426–1439. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/ddi.12778>.
- San Miguel Ayanz, J., D. de Rigo, G. Caudullo, T. H. Durrant, and A. Mauri. 2016. European Atlas of forest tree species. Publications Office of the European Union.
- Seidl, R., P. Baier, W. Rammer, A. Schopf, and M. J. Lexer. 2007. Modelling tree mortality by bark beetle infestation in Norway spruce forests. *Ecological Modelling* **206**:383–399.
- Shparyk, Y. S., R. Viter, and V. Y. Shparyk. 2018. Influence of natural factors on the dynamics of the beech (*Fagus sylvatica* L.) virgin forest of the Ukrainian Carpathians. *Scientific Bulletin of the UNFU* **28**:13–16.

- Stiers, M., K. Willim, D. Seidel, M. Ehbrecht, M. Kabal, C. Ammer, and P. Annighöfer. 2018. A quantitative comparison of the structural complexity of managed, lately unmanaged and primary European beech (*Fagus sylvatica* L.) forests. *Forest Ecology and Management* **430**:357–365.
- Trotsiuk, V., M. L. Hobi, and B. Commarmot. 2012. Age structure and disturbance dynamics of the relic virgin beech forest Uholka (Ukrainian Carpathians). *Forest Ecology and Management* **265**:181–190.
- Tsykun, T., D. Rigling, V. Nikolaychuk, and S. Prospero. 2012. Diversity and ecology of *Armillaria* species in virgin forests in the Ukrainian Carpathians. *Mycological progress* **11**:403–414.
- van der Maaten-Theunissen, M., H.-P. Kahle, and E. van der Maaten. 2013. Drought sensitivity of Norway spruce is higher than that of silver fir along an altitudinal gradient in southwestern Germany. *Annals of Forest Science* **70**:185–193.
- von Oheimb, G., C. Westphal, H. Tempel, and W. Härdtle. 2005. Structural pattern of a near-natural beech forest (*Fagus sylvatica*)(Serrahn, North-east Germany). *Forest Ecology and Management* **212**:253–263.
- Wiegand, T., S. Gunatilleke, and N. Gunatilleke. 2007. Species associations in a heterogeneous Sri Lankan dipterocarp forest. *The American Naturalist* **170**:E77–E95.
- Willim, K., M. Stiers, P. Annighöfer, C. Ammer, M. Ehbrecht, M. Kabal, J. Stillhard, and D. Seidel. 2019. Assessing Understory Complexity in Beech-dominated Forests (*Fagus sylvatica* L.) in Central Europe—From Managed to Primary Forests. *Sensors* **19**:1684.
- Zenner, E. K., J. E. Peck, M. L. Hobi, and B. Commarmot. 2015. The dynamics of structure across scale in a primaeval European beech stand. *Forestry* **88**:180–189.
- Zenner, E. K., J. E. Peck, M. L. Hobi, and B. Commarmot. 2016. Validation of a classification protocol: meeting the prospect requirement and ensuring distinctiveness when assigning forest development phases. *Applied Vegetation Science* **19**:541–552.