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Tree-ring reconstruction of forest disturbances: evaluation of methods and past changes on forest dynamic

Ph.D. Thesis

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Annotation

Tree-ring data serves as a chronicle of the past environment and provides long-term records about climate variations, volcanic eruptions, glacial activity and many others processes. Over the past few decades, dendrochronology has become common in studying disturbances. This thesis is focused on release detection methods (i.e. abrupt growth after death of neighbouring tree(s)) and their application. The presented review showed that despite the some uncertainties in methodological approaches, release detection is a reliable tool for forest disturbance reconstruction. In this thesis, release detection was applied in various forest ecosystems for reconstruction of disturbances and their effects. The achieved results importantly contribute to the understanding of the ecological processes concerning forest management, long-term changes in natural forest ecosystems, forest diversity and the impact of global changes.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury. Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

I. **Altman J.**, Doležal J., Černý T. & Song J.S. (2013) Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings. *Global Change Biology* **19**: 498–504 (IF = 8.224).
Jan Altman was responsible for experimental design, laboratory work, data assembly, data analysis and writing and revision of the manuscript and participated in data collection in the field.

II. **Altman J.**, Hédl R., Szabó P., Mazůrek P., Riedl V., Müllerová J., Kopecký M. & Doležal J. (2013) Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in Central Europe. *PLoS ONE* **8(2)**: e55770 (IF = 3.534).
Jan Altman was responsible for dendrochronological analysis, writing and revision of the manuscript and participated on experiment preparation and neighborhood analysis.

III. **Altman, J.**, Fibich, P., Dolezal, J. & Aakala, T. (2014) TRADER: a package for Tree Ring Analysis of Disturbance Events in R. *Dendrochronologia*, **32**: 107-112 (IF = 1.697).
Jan Altman was fully responsible for writing of the manuscript.

IV. **Altman J.**, Dolezal J., Fibich P., Leps J., Uemura S. & Hara T. Impact of typhoons on forest dynamic over 230 years: spatiotemporal analysis of past disturbances and tree establishment (*submitted manuscript*).
Jan Altman was responsible for dendrochronological analysis and writing of the manuscript.

Contents

Chapter I

General introduction

Photo on previous page: a growth rings of *Picea abies* with example of release, which is indicated by abrupt increase in growth (two-thirds on the left side) after the period of suppression (very narrow rings on the right third).

General introduction

In this chapter of the thesis, I aim to summarize the current knowledge of the reconstruction of disturbance events by means of tree-ring data. Specifically, I will focus on the methods and their strengths and limitations. The ecological application of the results and the future challenges in this branch of science will also be discussed. To lay the foundations, I will briefly introduce dendrochronology, and cover the basic principles, concepts and applications of tree-ring science.

1. Dendrochronology

Humankind is fascinated by history and every discovery about past processes provides an improvement of general knowledge. While direct records of historical processes are rather limited from a long-term perspective, attention should be focused on natural archives such as glaciers, sediments or living organisms forming annual growth layers. Woody plants with secondary growth form annual rings in the xylem, commonly known as *tree-rings*, which mirror the variety of environmental and ecophysiological conditions that they experience during growth. Tree-rings therefore serve as fingerprints of past processes and provide long-term records of past climate variations (e.g. Buntgen *et al.*, 2011), insect outbreaks (e.g. Paritsis & Veblen, 2011), volcanic eruptions (e.g. Briffa *et al.*, 1998), glacial activity (e.g. Dolezal *et al.*, 2014), landslides (e.g. Saez *et al.*, 2012) and many others (see Schweingruber, 1996; Speer, 2010; Stoffel, 2010).

The scientific discipline dealing with tree-rings is called *dendrochronology*. The real meaning of the word "dendrochronology" is found in its Greek roots: *dendron* = tree, *chronology* = the study of time. In the broad sense, dendrochronology is a science that applies the information content in the structure of tree-rings dated to the exact years of their formation for the analysis of environmental, ecological, ecophysiological and historical processes. As the scope of dendrochronology is fairly extensive, many subfields have been developed: dendroarchaeology, dendroclimatology, dendroecology, dendrogeomorphology, and dendrochemistry (for details see Speer (2010)).

From my own experience, people generally think that the main purpose of dendrochronology is the determination of the age of the trees. However, age in itself is really only interesting when exceptionally old individuals are recognized (see the OLDLIST http://www.rmtrr.org/oldlist.htm) and it is usually a by-product of tree-ring width measurement. The main (and most traditional) source of information used in dendrochronology represents just tree-ring widths. For deriving more detailed data, early and late wood widths can be measured separately in some species. In some studies, it can be more useful to calculate the basal area increment (expressed as mm^2/year) (see Visser, 1995).

After tree-ring width measurement, the basic tenet of dendrochronology, which is called *crossdating* is usually applied. The principal of crossdating is that to each individual tree-ring is assigned the its exact year of formation. This is performed by matching the patterns of wide and narrow rings between cores from the same tree, between individual trees from one locality and subsequently even between trees from different localities. When tree-ring series are crossdated, average series representing the stand level or regional signal can be developed. Such an average series is called the *master chronology* or just simply the *chronology*. Long-term chronologies have been constructed by the combination of tree-ring series from living trees and dead trees, i.e. wooden beams used for constructions and archaeological structures themselves or trees preserved in arid condition or in anaerobic conditions e.g. in deeper layers of bogs. Currently, the longest chronology (combined oak and pine) extends back 12,460 years and covers the entire Holocene and 820 years of the Younger Dryas (Friedrich *et al.*, 2004). These long, precisely dated series with annual resolution were also used for the calibration of radiocarbon dating and considerably improved its accuracy (Pilcher, 1984; Kromer, 2009).

Tree-ring widths are not the only source of information used in dendrochronology. In the early 1960s, Polge (1963) introduced wood densitometry and over the subsequent years this method was further developed (Polge, 1978; Schweingruber *et al.*, 1978; Schweingruber, 1990; Bergsten *et al.*, 2001; Schinker *et al.*, 2003; Van den Bulcke *et al.*, 2014). Wood density variation provides more accurate results than tree-ring widths. More specifically, maximum latewood density seems to be a reliable predictor for the reconstruction of temperature and precipitation (e.g. Hughes *et al.*, 1994; Battipaglia *et al.*, 2010). Moreover, density variations have been also utilized for the reconstruction of anthropogenic pollutions (Ferretti *et al.*, 2002) and tree-ring boundary identification in tropical trees with barely visibly tree-rings (Worbes, 2002). Recently a new tree-ring parameter – blue intensity – which could be used as an alternative to maximum latewood density was described (McCarroll *et al.*, 2002; Campbell *et al.*, 2007; Wilson *et al.*, 2014). Blue intensity provides an inexpensive and accessible alternative to density measurement, which is restricted to a relatively small number of laboratories.

Another tool increasingly used in dendrochronology are stable isotopes. Ratios of stable isotopes in tree-ring cellulose or whole wood provide a detailed retrospective insight into ecophysiological processes (McCarroll & Loader, 2004; Gessler *et al.*, 2014). The most utilized are carbon and oxygen isotope ratios ($\delta^{13}C$ and $\delta^{18}O$ respectively), but others (hydrogen, nitrogen) are also employed. Very high-resolution sampling may hold the key for the reconstruction of physiological processes from tropical trees which lack tree-rings (McCarroll & Loader, 2004; Rozendaal & Zuidema, 2011). However, as Gessler *et al.* (2014) pointed out, there are still uncertainties, which must be resolved to provide a more complex insight into the ecophysiological processes from leaf to wood formation.

Recently, wood anatomical variables (such as the size of conducting tissues, cell wall thickness *etc.*) have been used in dendrochronology and are providing promising results (e.g. Bauerle *et al.*, 2011; Fonti *et al.*, 2010; Olano *et al.*, 2013). The basic methods of dendrochronology have also been recently applied to shrubs and herbs with distinct growth rings (e.g. Dietz & von Arx, 2005; Schweingruber *et al.*, 2011). Such changes require the redefinition of commonly-used terms (e.g. stem anatomy instead of wood anatomy) and suggest the semantic broadening of 'dendrochronology' towards 'xylemchronology' (Schweingruber & Buentgen, 2013). Moreover, the principles of dendrochronology are also used more frequently and efficiently on animals with annual growth rings (e.g. Butler *et al.*, 2013; Buntgen *et al.*, 2014; Richard *et al.*, 2014; Rountrey, 2014).

As obvious from above, dendrochronology covers an enormous variety of methods, which are constantly increasing. Dendrochronology has obvious advantages in comparison with other natural archives such as sediments, peatbog and ice cores, however, as in all scientific fields, there are also certain limitations (Speer, 2010). Researchers in dendrochronology are investigating most areas of natural science and making dendrochronology more and more interdisciplinary. Such applications make dendrochronology a useful research field which contributes enormously to the knowledge of the natural world.

1. *Tree-rings and disturbances*

This part is the subject of unpublished manuscript. The full version of this part of Chapter I is archived by the Faculty of Science, University of South Bohemia in the printed version of the Ph.D. Thesis.

3. Objectives and content of the thesis

In this thesis I focused on disturbance reconstruction by studying tree-rings. The thesis can be divided into two parts. The first part is methodological and consists of the first two chapters. The second part, which consists of the three remaining chapters, is focused on disturbance reconstruction and its ecological implications in both managed and natural forest ecosystems.

Chapter 1 presents a review of current knowledge about release detection with emphasis on methodological approaches, weakness and strengths of most common methods, and future challenges in this scientific field.

Chapter 2 contains a partial review of the methods used for release reconstruction and chiefly provides a unique tool, the TRADER package, which enables the analysis of disturbance history and functions for the detection of tree recruitment and growth trends.

Chapter 3 reconstructs disturbances in a former coppice-with-standards from tree-rings of oak standards, to link coppicing events with the recruitment of mature oaks, and to determine the effects of neighbouring trees on the stem increment of oak standards.

Chapter 4 examines long-term changes in typhoon frequency and intensity along latitudinal gradients in South Korea, explores how individual characteristics of typhoons affects the frequency of release events in old-growth oak forests, and reconstructs the frequency of release events in the past 200 years.

Chapter 5 explores the impact of severe and intermediate wind disturbances on tree recruitment and diversity in an oak-fir-maple forest in time (over the 230 years) and space.

Chapter 6 summarises the main results of this thesis.

4. References

Abrams MD, Copenheaver CA, Terazawa K, Umeki K, Takiya M, Akashi N (1999) A 370-year dendroecological history of an old-growth *Abies-Acer-Quercus* forest in Hokkaido, northern Japan. *Canadian Journal of Forest Research,* **29**, 1891-1899.

Altman J, Dolezal J, Cerny T, Song JS (2013a) Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings. *Global Change Biology,* **19**, 498-504.

Altman J, Fibich P, Dolezal J, Aakala T (2014) TRADER: a package for Tree Ring Analysis of Disturbance Events in R. *Dendrochronologia,* **32**, 107-112.

Altman J, Hedl R, Szabo P *et al.* (2013b) Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in central Europe. *Plos One,* **8**, e55770.

Asner GP (2013) Geography of forest disturbance. *Proceedings of the National Academy of Sciences of the United States of America,* **110**, 3711-3712.

Battipaglia G, Frank D, Buntgen U, Dobrovolny P, Brazdil R, Pfister C, Esper J (2010) Five centuries of Central European temperature extremes reconstructed from tree-ring density and documentary evidence. *Global and Planetary Change,* **72**, 182-191.

Bauerle TL, Centinari M, Bauerle WL (2011) Shifts in xylem vessel diameter and embolisms in grafted apple trees of differing rootstock growth potential in response to drought. *Planta,* **234**, 1045-1054.

Bergsten U, Lindeberg J, Rindby A, Evans R (2001) Batch measurements of wood density on intact or prepared drill cores using x-ray microdensitometry. *Wood Science and Technology,* **35**, 435-452.

Black BA, Abrams MD (2003) Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications,* **13**, 1733-1749.

Black BA, Abrams MD, Gagen M, Daniels LD, Kipfmueller KF, Speer JH, Anchukaitis KJ (2004) Development and application of boundary-line release criteria. *Dendrochronologia,* **22**, 31-42.

Black BA, Abrams MD, Rentch JS, Gould PJ (2009) Properties of boundary-line release criteria in North American tree species. *Annals of Forest Science,* **66**.

Bosela M, Petras R, Sitkova Z *et al.* (2014) Possible causes of the recent rapid increase in the radial increment of silver fir in the Western Carpathians. *Environmental Pollution,* **184**, 211-221.

Briffa KR, Jones PD, Schweingruber FH, Osborn TJ (1998) Influence of volcanic eruptions on Northern Hemisphere summer temperature over the past 600 years. *Nature,* **393**, 450-455.

Buchanan ML, Hart JL (2011) A methodological analysis of canopy disturbance reconstructions using *Quercus alba*. *Canadian Journal of Forest Research,* **41**, 1359-1367.

Buntgen U, Liebhold A, Jenny H *et al.* (2014) European springtime temperature synchronises ibex horn growth across the eastern Swiss Alps. *Ecology Letters,* **17**, 303-313.

Buntgen U, Tegel W, Nicolussi K *et al.* (2011) 2500 years of European climate variability and human susceptibility. *Science,* **331**, 578-582.

Butler PG, Wanamaker AD, Scourse JD, Richardson CA, Reynolds DJ (2013) Variability of marine climate on the North Icelandic Shelf in a 1357-year proxy archive based on growth increments in the bivalve *Arctica islandica*. *Palaeogeography Palaeoclimatology Palaeoecology,* **373**, 141-151.

Campbell R, Mccarroll D, Loader NJ, Grudd H, Robertson I, Jalkanen R (2007) Blue intensity in *Pinus sylvestris* tree-rings: developing a new palaeoclimate proxy. *Holocene,* **17**, 821-828.

Canham CD (1990) Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club,* **117**, 1-7.

Casteller A, Stoeckli V, Villalba R, Mayer AC (2007) An evaluation of dendroecological indicators of snow avalanches in the Swiss Alps. *Arctic Antarctic and Alpine Research,* **39**, 218-228.

Cook JE (2000) Disturbance history of two natural areas in Wisconsin: Implications for management. *Natural Areas Journal,* **20**, 24-35.
Copenheaver CA, Black BA, Stine MB, Mcmanamay RH, Bartens J (2009) Identifying dendroecological growth releases in American beech, jack pine, and white oak: Within-tree sampling strategy. *Forest Ecology and Management,* **257**, 2235-2240.
Denslow JS (1987) Tropical rain-forest gaps and tree species-diversity. *Annual Review of Ecology and Systematics,* **18**, 431-451.
Dietz H, von Arx G (2005) Climatic fluctuation causes large-scale synchronous variation in radial root increments of perennial forbs. *Ecology,* **86**, 327-333.
Dolezal J, Altman J, Vetrova VP, Hara T (2014) Linking two centuries of tree growth and glacier dynamics with climate changes in Kamchatka. *Climatic Change,* **124**, 207-220.
Druckenbrod DL (2005) Dendroecological reconstructions of forest disturbance history using time-series analysis with intervention detection. *Canadian Journal of Forest Research,* **35**, 868-876.
Druckenbrod DL, Pederson N, Rentch J, Cook ER (2013) A comparison of times series approaches for dendroecological reconstructions of past canopy disturbance events. *Forest Ecology and Management,* **302**, 23-33.
Egnell G, Valinger E (2003) Survival, growth, and growth allocation of planted Scots pine trees after different levels of biomass removal in clear-felling. *Forest Ecology and Management,* **177**, 65-74.
Ferretti M, Innes JL, Jalkanen R, Saurer M, Schaeffer J, Spiecker H, von Wilpert K (2002) Air pollution and environmental chemistry: What role for tree-ring studies? *Dendrochronologia,* **20**, 159-174.
Fonti P, von Arx G, Garcia-Gonzalez I, Eilmann B, Sass-Klaassen U, Gartner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *New Phytologist,* **185**, 42-53.
Foster DR, Knight DH, Franklin JF (1998) Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems,* **1**, 497-510.
Fraver S, White AS (2005) Identifying growth releases in dendrochronological studies of forest disturbance. *Canadian Journal of Forest Research,* **35**, 1648-1656.
Frelich LE (2002) *Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests,* Cambridge, Cambridge University Press.
Friedrich M, Remmelel S, Kromer B *et al.* (2004) The 12,460-year Hohenheim oak and pine tree-ring chronology from central Europe - A unique annual record for radiocarbon calibration and paleoenvironment reconstructions. *Radiocarbon,* **46**, 1111-1122.
Gessler A, Ferrio JP, Hommel R, Treydte K, Werner RA, Monson RK (2014) Stable isotopes in tree rings: towards a mechanistic understanding of isotope fractionation and mixing processes from the leaves to the wood. *Tree Physiology*.
Glitzenstein JS, Harcombe PA, Streng DR (1986) Disturbance, succession, and maintenance of species-diversity in an east Texas forest. *Ecological Monographs,* **56**, 243-258.
Hart JL, Grissino-Mayer HD (2008) Vegetation patterns and dendroecology of a mixed hardwood forest on the Cumberland Plateau: Implications for stand development. *Forest Ecology and Management,* **255**, 1960-1975.
Hart JL, van De Gevel SL, Sakulich J, Grissino-Mayer HD (2010) Influence of climate and disturbance on the growth of *Tsuga canadensis* at its southern limit in eastern North America. *Trees-Structure and Function,* **24**, 621-633.
Henry JD, Swan JMA (1974) Reconstructin forest history from live and dead plant material - an approach to study of forest succession in southwest New Hamshire. *Ecology,* **55**, 772-783.
Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion - implications for conservations. *Conservation Biology,* **6**, 324-337.

Hughes MK, Wu XD, Shao XM, Garfin GM (1994) A preliminary reconstruction of rainfall in north-central China since ad 1600 from tree-ring density and width. *Quaternary Research,* **42**, 88-99.

Ishikawa Y, Krestov PV, Namikawa K (1999) Disturbance history and tree establishment in old-growth *Pinus koraiensis*-hardwood forests in the Russian Far East. *Journal of Vegetation Science,* **10**, 439-448.

Kellner JR, Asner GP, Vitousek PM, Tweiten MA, Hotchkiss S, Chadwick OA (2011) Dependence of forest structure and dynamics on substrate age and ecosystem development. *Ecosystems,* **14**, 1156-1167.

Kromer B (2009) Radiocarbon and dendrochronology. *Dendrochronologia,* **27**, 15-19.

Leak WB (1987) Comparison of standard and actual tree-growth trends for deciduous and coniferous species in New Hampshire. *Canadian Journal of Forest Research,* **17**, 1297-1300.

Li ZQ, Bogaert J, Nijs I (2005) Gap pattern and colonization opportunities in plant communities: effects of species richness, mortality, and spatial aggregation. *Ecography,* **28**, 777-790.

Lorimer CG (1985) Methodological considerations in the analysis of forest disturbance history. *Canadian Journal of Forest Research,* **15**, 200-213.

Lorimer CG, Dahir SE, Singer MT (1999) Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. *Plant Ecology,* **143**, 189-202.

Lorimer CG, Frelich LE (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. *Canadian Journal of Forest Research,* **19**, 651-663.

Lorimer CG, Frelich LE, Nordheim EV (1988) Estimating gap origin probabilities for canopy trees. *Ecology,* **69**, 778-785.

Läänelaid A, Sohar K, Kull A (2014) Assessment of required buffer zones around mires in Estonia. In: *WorldDendro 2014.* (ed Baker P), Melbourne, Australia.

Mccarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quaternary Science Reviews,* **23**, 771-801.

Mccarroll D, Pettigrew E, Luckman A, Guibal F, Edouard JL (2002) Blue reflectance provides a surrogate for latewood density of high-latitude pine tree rings. *Arctic Antarctic and Alpine Research,* **34**, 450-453.

Mclachlan JS, Foster DR, Menalled F (2000) Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. *Ecology,* **81**, 717-733.

Middendorp RS, Vlam M, Rebel KT, Baker PJ, Bunyavejchewin S, Zuidema PA (2013) Disturbance history of a seasonal tropical forest in western Thailand: a spatial dendroecological analysis. *Biotropica,* **45**, 578-586.

Misson L, Vincke C, Devillez F (2003) Frequency responses of radial growth series after different thinning intensities in Norway spruce (*Picea abies* (L.) Karst.) stands. *Forest Ecology and Management,* **177**, 51-63.

Motta R, Nola P, Piussi P (1999) Structure and stand development in three subalpine Norway spruce (*Picea abies* (L.) Karst,) stands in Paneveggio (Trento, Italy). *Global Ecology and Biogeography,* **8**, 455-471.

Naaf T, Wulf M (2007) Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. *Forest Ecology and Management,* **244**, 141-149.

Nagel T, Levanic T, Diaci J (2007) A dendroecological reconstruction of disturbance in an old-growth *Fagus-Abies* forest in Slovenia. *Annals of Forest Science,* **64**, 891-897.

Nehrbass-Ahles C, Babst F, Klesse S *et al.* (2014) The influence of sampling design on tree-ring-based quantification of forest growth. *Global Change Biology,* **20**, 2867-2885.

Niukkanen L, Kuuluvainen T (2011) Radial growth patterns of dominant trees in two old-growth forests in eastern Fennoscandia. *Journal of Forest Research,* **16**, 228-236.

NOAA (2012) Contributors of the International Tree-Ring Data Bank, IGBP PAGES/World Data Center for Paleoclimatology, NOAA/NGDC Paleoclimatology Program. Boulder, Colorado, USA.

Nowacki GJ, Abrams MD (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs,* **67**, 225-249.

Olano JM, Arzac A, Garcia-Cervigon AI, von Arx G, Rozas V (2013) New star on the stage: amount of ray parenchyma in tree rings shows a link to climate. *New Phytologist,* **198**, 486-495.

Paritsis J, Veblen TT (2011) Dendroecological analysis of defoliator outbreaks on *Nothofagus pumilio* and their relation to climate variability in the Patagonian Andes. *Global Change Biology,* **17**, 239-253.

Payette S, Filion L, Delwaide A (1990) Disturbance regime of a cold temperate forest as decuded from tree-ring patterns: the Tantare Ecological Reserve, Quebec. *Canadian Journal of Forest Research,* **20**, 1228-1241.

Pederson N, Dyer JM, Mcewan RW *et al.* (2014) The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecological Monographs*. http://dx.doi.org/10.1890/13-1025.1

Pickett STA, White PS (1985) *The ecology of natural disturbance and patch dynamics,* New York, Academic Press.

Pilcher JR, Bailie MGL, Schmidt B, Becker B (1984) A 7272-year tree-ring chronology for western Europe. *Nature,* **5990**, 150 - 152

Polge H (1963) Une nouvelle méthode de détermination de la texture du bois-L'analyse densitométrique de clichés radiographiques. *Annals of forest science,* **20**, 533-580.

Polge H (1978) Fifteen years of wood radiation densitometry. *Wood Science and Technology,* **12**, 187-196.

Rentch JS, Desta F, Miller GW (2002) Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, USA. *Canadian Journal of Forest Research,* **32**, 915-927.

Richard MG, Laroque CP, Herman TB (2014) Relating annual increments of the endangered Blanding's turtle plastron growth to climate. *Ecology and Evolution,* **4**, 1972-1980.

Romme WH, Everham EH, Frelich LE, Moritz MA, Sparks RE (1998) Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems,* **1**, 524-534.

Rountrey AN, Coulson PG, Meeuwig JJ, Meekan M (2014) Water temperature and fish growth: otoliths predict growth patterns of a marine fish in a changing climate. *Global Change Biology*, **20**, 2450-2458.

Rozendaal DMA, Zuidema PA (2011) Dendroecology in the tropics: a review. *Trees-Structure and Function,* **25**, 3-16.

Rubino DL, Mccarthy BC (2004) Comparative analysis of dendroecological methods used to assess disturbance events. *Dendrochronologia,* **21**, 97-115.

Rydval M, Wilson R (2012) The impact of industrial SO_2 pollution on north bohemia conifers. *Water Air and Soil Pollution,* **223**, 5727-5744.

Rykiel EJ (1985) Towards a definition of ecological disturbance. *Australian Journal of Ecology,* **10**, 361-365.

Saez JL, Corona C, Stoffel M, Schoeneich P, Berger F (2012) Probability maps of landslide reactivation derived from tree-ring records: Pra Bellon landslide, southern French Alps. *Geomorphology,* **138**, 189-202.

Samonil P, Antolik L, Svoboda M, Adam D (2009) Dynamics of windthrow events in a natural fir-beech forest in the Carpathian mountains. *Forest Ecology and Management,* **257**, 1148-1156.

Samonil P, Dolezelova P, Vasickova I *et al.* (2013) Individual-based approach to the detection of disturbance history through spatial scales in a natural beech-dominated forest. *Journal of Vegetation Science,* **24**, 1167-1184.

Schinker MG, Hansen N, Spiecker H (2003) High-frequency densitometry - a new method for the rapic evaluation of wood density variations. *Iawa Journal,* **24**, 231-239.

Schweingruber FH (1990) Radiodensitometry. In: *Methods of dendrochronology* (eds Cook Er, Kairiukstis A) pp 55-63. Dordrecht, Kluwer.
Schweingruber FH (1996) *Tree rings and environment: Dendroecology*, Berne, Paul Haupt AG Bern.
Schweingruber FH, Boerner A, Schulze ED (2011) *Atlas of Stem Anatomy in Herbs, Shrubs and Trees, Volume 1*, Springer-Verlag, Berlin, Germany.
Schweingruber FH, Buentgen U (2013) What is 'wood' - An anatomical re-definition. *Dendrochronologia,* **31**, 187-191.
Schweingruber FH, Fritts HC, Bräker OU, Drew LG, Schär E (1978) The X-Ray technique as applied to dendroclimatology. *Tree-Ring Bulletin,* **1978**, 61-91.
Shimatani IK, Kubota Y (2011) The spatio-temporal forest patch dynamics inferred from the fine-scale synchronicity in growth chronology. *Journal of Vegetation Science,* **22**, 334-345.
Speer JH (2010) *Fundamentals of Tree-ring Research*, University of Arizona Press.
Splechtna BE, Gratzer G, Black BA (2005) Disturbance history of a European old-growth mixed-species forest - A spatial dendro-ecological analysis. *Journal of Vegetation Science,* **16**, 511-522.
Stoffel M (2006) A review of studies dealing with tree rings and rockfall activity: the role of dendrogeomorphology in natural hazard research. *Natural Hazards,* **39**, 51-70.
Stoffel M (2010) *Tree rings and natural hazards: a state-of-art*, Springer.
Stoffel M, Bollschweiler M (2008) Tree-ring analysis in natural hazards research - an overview. *Natural Hazards and Earth System Sciences,* **8**, 187-202.
Svoboda M, Janda P, Bače. R *et al.* (2014) Landscape-level variability in historical disturbance in primary *Picea abies* mountain forests of the Eastern Carpathians, Romania. *Journal of Vegetation Science,* **25**, 386--401.
Takaoka S (1993) The effect of missing rings on stand-age estimation of even-aged forests in northern Hokkaido, Japan. *Ecological Research,* **8**, 341-347.
Tardif J, Bergeron Y (1999) Population dynamics of *Fraxinus nigra* in response to flood-level variations, in Northwestern Quebec. *Ecological Monographs,* **69**, 107-125.
Thompson RD, Daniels LD, Lewis KJ (2007) A new dendroecological method to differentiate growth responses to fine-scale disturbance from regional-scale environmental variation. *Canadian Journal of Forest Research,* **37**, 1034-1043.
Turner MG, Dale VH (1998) Comparing large, infrequent disturbances: what have we learned? *Ecosystems,* **1**, 493-496.
van Den Bulcke J, Wernersson ELG, Dierick M *et al.* (2014) 3D tree-ring analysis using helical X-ray tomography. *Dendrochronologia,* **32**, 39-46.
Veblen Tt (1986) Treefalls and the coexistence of conifers in sub-alpine forests of the central Rockies. *Ecology,* **67**, 644-649.
Visser H (1995) Note on the relation between ring widths and basal area increments. *Forest Science,* **41**, 297-304.
Webster CR, Jensen NR (2007) A shift in the gap dynamics of *Betula alleghaniensis* in response to single-tree selection. *Canadian Journal of Forest Research,* **37**, 682-689.
Wilson R, Rao R, Rydval M, Wood C, Larsson LÅ, Luckman BH (2014) Blue Intensity for dendroclimatology: The BC blues: A case study from British Columbia, Canada. *The Holocene*.
Winter LE, Brubaker LB, Franklin JF, Miller EA, Dewitt DQ (2002) Canopy disturbances over the five-century lifetime of an old-growth Douglas-fir stand in the Pacific Northwest. *Canadian Journal of Forest Research,* **32**, 1057-1070.
Worbes M (2002) One hundred years of tree-ring research in the tropics - a brief history and an outlook to future challenges. *Dendrochronologia,* **20**, 217-231.
Zhang JW, Oliver WW (2006) Stand structure and growth of *Abies magnifica* responded to five thinning levels in northeastern California, USA. *Forest Ecology and Management,* **223**, 275-283.

Ziaco E, Biondi F, Di Filippo A, Piovesan G (2012) Biogeoclimatic influences on tree growth releases identified by the boundary line method in beech (*Fagus sylvatica* L.) populations of southern Europe. *Forest Ecology and Management,* **286**, 28-37.
Zielonka T, Holeksa J, Fleischer P, Kapusta P (2010) A tree-ring reconstruction of wind disturbances in a forest of the Slovakian Tatra Mountains, Western Carpathians. *Journal of Vegetation Science,* **21**, 31-42.

Chapter II

TRADER: a package for Tree Ring Analysis of Disturbance Events in R.

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Photo on previous page: disturbance in the forest dominated by *Abies koreana* after the occurence of typhoon Bolaven in August 2012, Hallasan Mountains, Jeju Island, South Korea.

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Original article

TRADER: A package for Tree Ring Analysis of Disturbance Events in R

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ABSTRACT

Studies using tree-rings to reconstruct forest disturbance dynamics are common and their number has been increasing in the recent years. Despite the evident need for a common set of tools for verification, replication and comparison across studies, only a few DOS programmes for disturbance detection exist and they are for limited purposes only. Currently, the ideal statistical environment for the task is R, which is becoming the primary tool for various types of tree-ring analyses. This has led to the development of TRADER (Tree Ring Analysis of Disturbance Events in R), an open-source software package for R that provides an analysis of tree growth history for disturbance reconstructions. We have implemented four methods, which are commonly used for the detection of disturbance events: radial-growth averaging criteria developed by Nowacki and Abrams, 1997, the boundary-line method (Black and Abrams, 2003), the absolute-increase method (Fraver and White, 2005), and the combination of radial-growth averaging and boundary-line techniques (Splechtna et al., 2005). TRADER, however, enables the analysis of disturbance history by a total of 24 published methods. Furthermore, functions for the detection of tree recruitment and growth trends were also included. The main features of the presented package are described and their application is shown on a real tree-ring datasets. The package requires little knowledge of the R environment giving straightforward analyses with suitable parameters, but at the same time it is easily modifiable by the more experienced user. The package improves research efficiency and facilitates replication of previous studies. One of its major advantages is that it offers the possibility for comparison between different methods of disturbance history reconstruction.

Introduction

Dendrochronology has changed rapidly during the last century. From its basic beginnings in matching ring-width patterns across trees (crossdating) (e.g. Douglass, 1920, 1941), it has developed into one of the most precise tools for studying environmental processes (e.g. Buntgen et al., 2011; Altman et al., 2013a; Williams et al., 2013). With the continuing development of methods in dendrochronology, the need for better software has become apparent. Since the 1960s, dendrochronologists have made software freely available to the tree-ring community primarily as stand-alone programs (Holmes, 1983; Cook and Holmes, 1996), but also in other formats such as MATLAB-functions (Meko, 2002).

The R statistical software (R Development Core Team, 2013) has become a dominant platform across various fields of science (e.g. Boettiger and Lang, 2012; Adams and Otárola-Castillo, 2013; Cox et al., 2013). The main reason is its versatility, being both a programming language and software for statistical computing. It is also free, open-source, and developed by an active community. Dendrochronologist have worked within this platform and the most important functions have been adapted and ported into the R environment (Bunn, 2008, 2010; Campelo et al., 2012; Zang and Biondi, 2013). Unlike the tradition of using stand-alone software, this shift to R has the potential to facilitate improved verification, repeatability and improvement of methods by individual scientists.

Some of the sub-fields of dendrochronology, including the analysis of forest disturbance histories from tree-ring data, lack common software. In these analyses, series of tree-ring width measurements are often searched for the particular patterns which indicate disturbance in the canopy, as these disturbances influence resource availability and the growth rate of trees. As these methods are relatively new, there are only a few tools for the reconstruction

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of disturbance events, which are in DOS and are determined for specific applications (e.g. Holmes and Swetnam, 1996; Holmes, 1999). The lack of common tools for disturbance analysis has been discussed on the International Dendrochronology Discussion Forum (https://itrdbfor.org/) and dendrochronologists have been looking for suitable software, specifically in the R environment. A review by Rubino and McCarthy, 2004 explored the dendroecological methods used for the detection of historical disturbance events and found 28 different methods used for the identification and description of disturbance history. Since then, additional criteria and modifications have been developed to overcome some of the limitations of the early methods (e.g. Black and Abrams, 2003; Fraver and White, 2005). The high diversity of methods has resulted in substantial differences in the disturbance history reconstructions based the same data (Rubino and McCarthy, 2004). This clearly indicates the need for more transparent and verifiable methods of analysis.

Here we present TRADER (Tree Ring Analysis of Disturbance Events in R) - a package for R (R Development Core Team, 2013) that allows the reconstruction of disturbances from tree-ring data. The key features of the package are:

1. Predefined functions for four commonly used and accepted techniques, and the possibility for changing any of the analysis parameters. This enables the analysis of disturbance history of the forest by a total of 24 published methods (Supplementary Table 1).
2. Graphical outputs, which allow visual verification of the detected disturbances for individual tree-ring series. The functions also produce tables summarizing the analysis and the results.
3. Complementary analyses, which allow the determination of growth trends and the detection of tree establishment.

Rationale behind selected functions and their description

Methods for disturbance detection based on tree-ring data can be divided into two fundamental categories: (1) trees that were directly affected by the disturbance with the detection of these events made directly during the process of tree-ring analysis (e.g. fire scars, reaction wood) and (2) trees that were not directly affected by the disturbance, but had their growth influenced by the disturbed, close neighbourhood. All of the methods for disturbance detection relating to the 2nd category are based on the fact that trees which experience improved light conditions after the death of neighbouring trees react with an abrupt and sustained increase in their radial growth, reflecting their newly-attained position in the canopy (Lorimer and Frelich, 1989). This process is called release. Releases are commonly identified by an increased radial growth exceeding a predefined threshold. The majority of methods subdivide releases into "moderate" and "major" categories, to better distinguish mild disturbances from severe ones (Black and Abrams, 2003). A relatively large number of methods has been developed for release detection in the past (Rubino and McCarthy, 2004; Black et al., 2009), including some recent additions (Druckenbroad et al., 2013). In the TRADER-package, we included four methods which have been commonly used and verified across different kind of species, forests and areas.

According to the review made by Rubino and McCarthy, 2004, methods using the running mean (i.e. based on the comparison of the mean growth rate of adjacent groups of tree-rings) are the most abundant for the detection of disturbance events. The implementation of *radial-growth averaging criteria*, developed by Nowacki and Abrams, 1997, is one of the most commonly used techniques based on the running mean. In this approach, the average radial growth over the preceding 10-year period, M_1 (including the target year), and the average radial growth over the subsequent 10-year period, M_2 (excluding the target year) are computed, and the percentage growth change (%GC) is obtained by: $\%GC = [(M_2 - M_1)/M_1] \times 100$. The minimum thresholds applied for releases are typically a 25% growth change for moderate and >50% for major releases. The advantage of this method is its broad applicability even for a small number of samples, and that information about species autecology is not necessary. On the other hand, the generality of radial-growth averaging may lead to both the detection of false releases and the exclusion of true releases (Black and Abrams, 2003; Fraver and White, 2005). These inaccuracies are primarily caused by different growth rates in young, small and suppressed trees when compared to older, larger and dominant ones. In the TRADER package, this method is calculated by the function `growthAveragingALL`.

Recognizing the limitations of radial-growth averaging, additional criteria have been developed to fix different growth rates during the lifespan of individual trees within a species. Black and Abrams, 2003 presented the *boundary-line method*, which scales the percentage growth change of Nowacki and Abrams, 1997 according the growth rate prior to disturbance. In their example, Black and Abrams, 2003 defined moderate and major releases as those falling within 20–49.9%, and 50–100% of the boundary-line, respectively. The advantage of the boundary-line is standardization, as the scaling of percentage growth change to prior growth accounts for the relationships between tree age, size, and canopy class, which all influence the radial growth rate (Black et al., 2004). One disadvantage is that Black et al., 2009 suggest approximately 50,000 ring width measurements are necessary for boundary-line determination for a given species (Black et al., 2009). In a literature search, we found 27 different boundary-line functions developed for 19 species (Supplementary Table 2). The boundary-line is calculated by the function `boundaryLineALL`.

Both techniques described above are based on the relative changes of sequential 10-yr ring-width averages. However, in cases where species autecology (mean growth rate, species sensitivity and range of growth responses) is well known, it is possible to determine the absolute threshold for release detection instead of thresholds based on relative growth. Fraver and White, 2005 developed the *absolute-increase method* as the alternative to the percentage-increase method. They observed that empirically determined absolute-increase thresholds for each species roughly corresponded to 1.25 times the standard deviation, or somewhat less than the 90% quantile of all absolute increases (Fraver and White, 2005). In comparison with the two above mentioned techniques, the absolute-increase method has only one threshold (i.e. no distinction between moderate and major releases). The absolute-increase is calculated by the function `absoluteIncreaseALL`.

The fourth technique included in the TRADER-package is a combination of radial-growth averaging and boundary-line techniques. This method was developed by Splechtna et al., 2005, and it has been useful in reducing the numbers of false releases. In their implementation, candidate releases were accepted only if the growth pulse exceeded a 50% growth change threshold, computed according to Nowacki and Abrams, 1997. Only these potential releases were then scaled relative to the boundary line (Splechtna et al., 2005). This technique is calculated by the function `splechtnaALL`.

In studies of forest disturbance history, release analyses are commonly used in combination with other methods, such as an analysis of tree recruitment dates (e.g. Aakala et al., 2011). Tree recruitment dates often lag behind the growth-releases, either due to delayed recruitment or difficulties in determining the exact germination year (Rozas, 2003; Altman et al., 2013b). In the TRADER-package, tree recruitment is computed by the function plotFirstYears. Finally, growth patterns of individual trees can be visualized in TRADER, which has been used in studies of stand structural complexity (e.g. Franklin et al., 2002; Frelich, 2002; Niukkanen and Kuuluvainen, 2011). In TRADER, fourth degree polynomial functions according to Niukkanen and Kuuluvainen, 2011 can be fitted to tree-ring series by the function plotGrowth.

TRADER in practice

Any release-detection technique should be evaluated against real radial-growth data, and modifications to the release detection parameters may be needed if the criteria seem overly sensitive or overly strict. This is commonly referred to as adjusting the sensitivity of the criteria (Lorimer and Frelich, 1989; Frelich and Lorimer, 1991; Fraver and White, 2005). For this reason, functions in TRADER produce graphs for all the analyzed ring-width series, including values of computed functions and raw measurement. These graphs are automatically produced in a working folder and compiled into tables of results; tree-ring data can be stored in many formats. In TRADER, these data can be read using any of the functions implemented in the dplR-package (i.e., `read.compact`, `read.crn`, `read.fh`, `read.rwl`, `read.tridas` and `read.tuscon`) (Bunn, 2008). Data stored in other formats can be converted to one of the required formats (we recommend .rwl format) by the TRiCYCLE application (Brewer et al., 2011). Final input data must only contain measurements, where series IDs are the column names and the years are the row names.

First, download and install the TRADER package (https://github.com/pavel-fibich/TRADER) and also install the dplR package (Bunn, 2008). For the presentation of the main functions we used either a dataset (relData) containing 15 chronologies (tree-ring width series) for sessile oak (*Quercus petraea*) of known disturbance history from the study by Altman et al., 2013b (relData1) or 192 spruce chronologies (relData2), if more series were necessary.

```
> install.packages ("C:/TRADER/TRADER_1.0.1.tar.gz", repos = NULL,
  type = "source") *works if downloaded package is saved in the
  folder "TRADER" directly on disc C:
> install.packages("dplR")
> library("TRADER")
> data(relData)
```

After this, analyses following the radial-growth averaging criteria of Nowacki and Abrams, 1997 can be performed. All parameters can be checked by following the selected criteria and changed, if

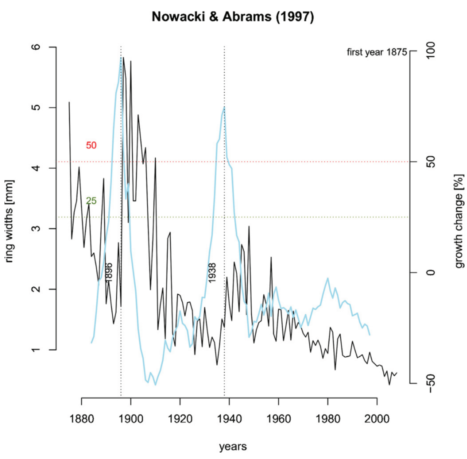

Fig. 1. Example of tree-ring series (tree ID 000031) with detected releases. Detected releases are in the years 1896 and 1938. Tree growth (black line) in individual years is displayed together with the function for release detection (blue line) with thresholds (red horizontal line for major releases exceeding 50% of percentage growth change and green horizontal line for moderate releases exceeding 25% of percentage growth change) according to Nowacki and Abrams, 1997. Year of the first measured tree-ring is indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

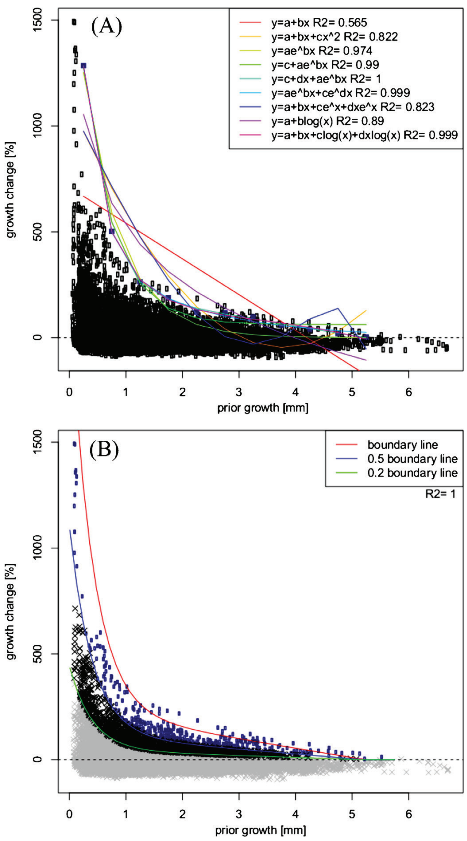

Fig. 2. (A) Individual fitted functions with coefficients of determination (R^2) for all tree-rings (black rectangles) are visualized by colour lines. (B) The function determining boundary-line (red line), thresholds for moderate (blue line) and major release (green line), and the all tree-ring data (years with values ≥50% of boundary-line = blue points, <50% and ≥20% = black cross, and <20% = grey cross). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

Table 1
Changeable parameters of individual functions with their predefined values and description. *RGA = radial-growth averaging (Nowacki and Abrams, 1997), BL = boundary-line (Black and Abrams, 2003), AI = absolute-increase (Fraver and White, 2005), and S = method of Splechtna et al., 2005. **NULL = if it is NULL, values of these parameters will be computed by defined criteria.

Parameter	Predefined values	Description	Relevant for function
m1	10	Determines the number of years to be averaged (including target year) for period prior the potential release	RGA, BL, AI, S
m2	10	Determines the number of years to be averaged (excluding target year) for period subsequent the potential release	RGA, BL, AI, S
criteria	0.25 (RGA) 0.2 (BL, S)	Threshold for detection of moderate release	RGA, BL, S
criteria2	0.5	Threshold for detection of major release	RGA, BL, S
boundary	NULL	Equation determining the boundary-line	BL, S
abs.threshold	NULL	Threshold of absolute-increase	AI
length	5	Determines how many years have to be given criteria exceeded to be considered as release	RGA, BL, AI, S
buffer	10	Number of years determining how close to one another two releases can be	RGA, BL, AI, S

necessary. The main options and changeable parameters for all four methods are explained and summarized in Table 1 and the rest are in Supplementary Table 3.

```
> growthAveragingALL(relData1, releases = NULL, m1 = 10, m2 = 10,
  buffer = 10, drawing = TRUE, criteria = 0.25, criteria2 = 0.5,
  prefix = "ga", gfun = mean, length = 5, storedev = jpeg)
```

This function produces a summary of all the analyses, including the parameters used, and the number of moderate (22 in the example) and major (16) releases and the number of releases in individual years (listed as moderate or major).

```
"## Nowacki & Abrams analysis!"
"Criteria 0.25 Criteria2 0.5 m1 10 m2 10 Buffer 10 Length 5"
"Total number of releases >= 0.25 is 22"
"Total number of releases >= 0.5 is 16"
```

In addition to the graphs for individual tree-ring series (Fig. 1), TRADER produces summary tables with computed functions for all tree-ring series as well as a synoptic table with the number of detected disturbances and sample depth. More information on these generated tables can be found in Supplementary Table 4.

The second method scales the percentage growth change to a boundary-line. The boundary-line can be built if there is a sufficient number of ring-width measurements available or an existing one can be used. These can be found in Supplementary Table 2 or displayed in R by command `knownBL`.

In our example, we will use the boundary-line determined for sessile oaks by Altman et al., 2013b: $y = 5.0067e^{-0.664x}$.

```
> boundaryLineALL(relData1, releases = NULL, m1 = 10, m2 = 10,
  boundary = function(x) {5.0067*exp(-0.664*x)}, buffer = 10,
  criteria = 0.2, criteria2 = 0.5, segment = 0.5, segment2 = 0.5,
  prefix = "bl", drawing = TRUE, gfun = mean, length = 5, notop = 10,
  notop2 = 10, storedev = jpeg)
```

The summary of the function displays the used parameters and also the number of moderate (19) and major (13) events. The number of releases in individual years is also shown.

```
"## Black & Abrams analysis!"
"Criteria 0.2 Criteria2 0.5 m1 10 m2 10 Buffer 10 Length 5
  Segment 0.5 Segment2 0.5"
"Total number of releases >= 0.2 is 19"
"Total number of releases >= 0.5 is 13"
```

If the equation of the boundary-line is unknown, TRADER fits nine different functions, which are visualized and coefficients of determination (R^2) are also shown (Fig. 2a). The best-fit function (or assigned one) is displayed with all the tree-ring data and the thresholds for moderate and major release (Fig. 2b). The computation of a new boundary-line to suit recorded data is described in detail in the Supplementary Information.

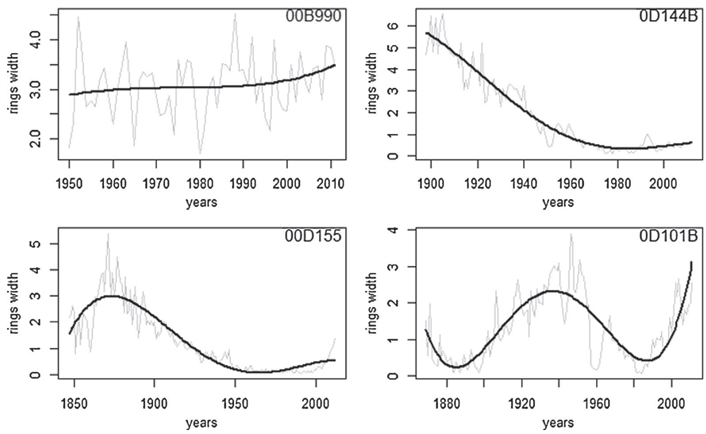

Fig. 3. Examples of different radial growth trends produced by function `plotGrowth`. Flat (tree ID 00B990), declining (tree ID 0D144B), and parabolic (tree ID 00D155 and 0D101B) radial increment patterns are shown.

The absolute-increase method is the last which will be introduced in detail. The known threshold of the absolute increase can be input directly or, if sufficient numbers of ring-width measurements are available, computed from the data. The computed threshold is 1.25 times the standard deviation of absolute increase, as suggested by Fraver and White, 2005.

```
> absoluteIncreaseALL(relData1, abs=NULL, m1=10, m2=10,
  buffer=10, prefix="ai", drawing=TRUE, gfun=mean, length=5,
  storedev=jpeg)
```

The resulting summary displays the parameters used and, more importantly, the value of the absolute-increase threshold and the number of detected releases.

```
"## Fraver & White analysis!"
"Absolute threshold 1.2 m1 10 m2 10 Buffer 10 Length 5"
"Total number of releases is 13"
```

The computation of the method developed by Splechtna et al., 2005 follows the process described for the boundary-line. We also included a function for computing all four methods at once, for obtaining a fast comparison of various methods and the sensitivity of the results to method selection. This analysis is calculated by calling the function `doAll`.

The complementary analysis of tree-establishment (i.e. the first year in the dataset) results in an automatically-saved table with the number of trees "established" each year. There is the possibility to load an optional vector containing series IDs in the first column (they must exactly match with series IDs in measurement) and information about the number of missing years in second column. This is required, for instance, if piths are missing from increment core samples. Analysis is made by the function:

```
> plotFirstYears (relData1, misspith= relMissPith)
```

Growth patterns that show the trends during the life history of individual trees requires visual classification. For this purpose, figures for individual growth series are created (Fig. 3). Plotting radial increments fitted by a fourth-degree polynomial function to the growth data is done by calling the function:

```
> plotGrowth (relData2, prefix="growth", polynom=4, store=TRUE,
  storedev=jpeg)
```

Conclusion

The TRADER package provides a unique method for disturbance reconstruction from tree-ring data. We developed TRADER in the open-source R environment to further support the on-going open-source software development for dendrochronological methods (e.g. Bunn, 2008; Jansma et al., 2010; Brewer et al., 2011) and data availability (NOAA, 2013). TRADER enables the analysis of disturbance history by a total of 24 published methods and functions for the detection of tree recruitment and growth trends were also included. The Final advantage of TRADER is the possibility of comparing results between individual studies. This is easily achieved by making parameter changes in the data processing and from the clearly arranged graphical and tabular outputs.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.dendro.2014.01.004.

References

Aakala, T., Kuuluvainen, T., Wallenius, T., Kauhanen, H., 2011. Tree mortality episodes in the intact *Picea abies*-dominated taiga in the Arkhangelsk region of northern European Russia. Journal of Vegetation Science 22, 322–333.
Adams, D.C., Otárola-Castillo, E., 2013. geomorph: an r package for the collection and analysis of geometric morphometric shape data. Methods in Ecology and Evolution 4, 393–399.
Altman, J., Dolezal, J., Cerny, T., Song, J.S., 2013a. Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings. Global Change Biology 19, 498–504.
Altman, J., Hedl, R., Szabo, P., Mazurek, P., Riedl, V., Mullerova, J., Kopecky, M., Dolezal, J., 2013b. Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in central Europe. PLoS One 8, e55770.
Black, B.A., Abrams, M.D., 2003. Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecological Applications 13, 1733–1749.
Black, B.A., Abrams, M.D., Gagen, M., Daniels, L.D., Kipfmueller, K.F., Speer, J.H., Anchukaitis, K.J., 2004. Development and application of boundary-line release criteria. Dendrochronologia 22, 31–42.
Black, B.A., Abrams, M.D., Rentch, J.S., Gould, P.J., 2009. Properties of boundary-line release criteria in North American tree species. Annals of Forest Science 66.
Boettiger, C., Lang, D.T., 2012. Treebase: an R package for discovery, access and manipulation of online phylogenies. Methods in Ecology and Evolution 3, 1060–1066.
Brewer, P.W., Murphy, D., Jansma, E., 2011. TRICYCLE: a universal conversion tool for digital tree-ring data. Tree-Ring Research 67, 135–144.
Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124.
Bunn, A.G., 2010. Statistical and visual crossdating in R using the dplR library. Dendrochronologia 28, 251–258.
Buntgen, U., Tegel, W., Nicolussi, K., McCormick, M., Frank, D., Trouet, V., Kaplan, J.O., Herzig, F., Heussner, K.U., Wanner, H., Luterbacher, J., Esper, J., 2011. 2500 years of European climate variability and human susceptibility. Science 331, 578–582.
Campelo, F., Garcia-Gonzalez, I., Nabais, C., 2012. detrendeR – a Graphical User Interface to process and visualize tree-ring data using R. Dendrochronologia 30, 57–60.
Cook, E.R., Holmes, R.L.,1996. Users Manual for Program ARSTAN. Laboratory of Tree-Ring Research. University of Arizona, Tucson, USA, p. 81.
Cox, M.J., Borchers, D.L., Kelly, N., 2013. nupoint: an R package for density estimation from point transects in the presence of non-uniform animal density. Methods in Ecology and Evolution 4, 589–594.
Douglass, A.E., 1920. Evidence of climatic effects in the annual rings of trees. Ecology 1, 24–32.
Douglass, A.E., 1941. Crossdating in dendrochronology. Journal of Forestry 39, 825–831.
Druckenbroad, D.L., Pederson, N., Rentch, J., Cook, E.R., 2013. A comparison of times series approaches for dendroecological reconstructions of past canopy disturbance events. Forest Ecology and Management 302, 23–33.
Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J.Q., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155, 399–423.
Fraver, S., White, A.S., 2005. Identifying growth releases in dendrochronological studies of forest disturbance. Canadian Journal of Forest Research 35, 1648–1656.
Frelich, L.E.,2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press, Cambridge, p. 266.
Frelich, L.E., Lorimer, C.G., 1991. Natural disturbance regimes in hemlock hardwood forests of the Upper Great Lakes region. Ecological Monographs 61, 145–164.
Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bulletin 43, 69–78.
Holmes, R.L.,1999. Program JOLTS: Finding Growth Surges or Suppressions in Trees. Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA, p. 65.
Holmes, R.L., Swetnam, T.W., 1996. Dendrochronology Program Library: Program OUTBREAK User's Manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, USA, 5 pp.
Jansma, E., Brewer, P.W., Zandhuis, I., 2010. TRiDaS 1.1: the tree-ring data standard. Dendrochronologia 28, 99–130.
Lorimer, C.G., Frelich, L.E., 1989. A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Canadian Journal of Forest Research 19, 651–663.
Meko, D., 2002. Tree-Ring MATLAB Toolbox, URL http://www.mathworks.com/matlabcentral/linkexchange/links/186-tree-ring-matlab-toolbox (accessed 15.12.13).

Niukkanen, L., Kuuluvainen, T., 2011. Radial growth patterns of dominant trees in two old-growth forests in eastern Fennoscandia. Journal of Forest Research 16, 228–236.

NOAA, 2013. Contributors of the International Tree-Ring Data Bank, IGBP PAGES/World Data Center for Paleoclimatology, NOAA/NGDC Paleoclimatology Program. Boulder, Colorado, USA.

Nowacki, G.J., Abrams, M.D., 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecological Monographs 67, 225–249.

R Development Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, URL http://www.R-project.org (accessed 15.12.13).

Rozas, V., 2003. Tree age estimates in *Fagus sylvatica* and *Quercus robur*: testing previous and improved methods. Plant Ecology 167, 193–212.

Rubino, D.L., McCarthy, B.C., 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21, 97–115.

Splechtna, B.E., Gratzer, G., Black, B.A., 2005. Disturbance history of a European old-growth mixed-species forest – a spatial dendro-ecological analysis. Journal of Vegetation Science 16, 511–522.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change 3, 292–297.

Zang, C., Biondi, F., 2013. Dendroclimatic calibration in R: the bootRes package for response and correlation function analysis. Dendrochronologia 31, 68–74.

Chapter III

Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in Central Europe

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Photo on previous page: abandoned coppice-with-standards with the detail on a spreading oak crown, South Moravia, Czech Republic.

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Tree-Rings Mirror Management Legacy: Dramatic Response of Standard Oaks to Past Coppicing in Central Europe

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Abstract

Background: Coppicing was one of the most important forest management systems in Europe documented in prehistory as well as in the Middle Ages. However, coppicing was gradually abandoned by the mid-20th century, which has altered the ecosystem structure, diversity and function of coppice woods.

Methodology/Principal Findings: Our aim was to disentangle factors shaping the historical growth dynamics of oak standards (i.e. mature trees growing through several coppice cycles) in a former coppice-with-standards in Central Europe. Specifically, we tried to detect historical coppicing events from tree-rings of oak standards, to link coppicing events with the recruitment of mature oaks, and to determine the effects of neighbouring trees on the stem increment of oak standards. Large peaks in radial growth found for the periods 1895–1899 and 1935–1939 matched with historical records of coppice harvests. After coppicing, the number of newly recruited oak standards markedly grew in comparison with the preceding or following periods. The last significant recruitment of oak standards was after the 1930s following the last regular coppicing event. The diameter increment of oak standards from 1953 to 2003 was negatively correlated with competition indices, suggesting that neighbouring trees (mainly resprouting coppiced *Tilia platyphyllos*) partly suppressed the growth of oak standards. Our results showed that improved light conditions following historical coppicing events caused significant increase in pulses of radial growth and most probably maintained oak recruitment.

Conclusions/Significance: Our historical perspective carries important implications for oak management in Central Europe and elsewhere. Relatively intense cutting creating open canopy woodlands, either as in the coppicing system or in the form of selective cutting, is needed to achieve significant radial growth in mature oaks. It is also critical for the successful regeneration and long-term maintenance of oak populations.

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Introduction

Knowledge about the long-term development of forests is essential both for a theoretical understanding of present composition and structure, and for practical issues of management and conservation of forest ecosystems. Tree-rings offer an excellent opportunity to investigate forest history; dendroecological methods provide high spatial and temporal resolution [1]. Over the past few decades, dendroecology has become common in studying disturbances in semi-natural forests and a wide range of methods has been developed for identifying such disturbances using tree-ring data. All of these methods are based on the fact that trees which experience improved light conditions after the falling of neighbouring trees react with an abrupt increase in radial growth. This process is called *release*. Release events are inferred from tree-ring series if growth exceeds a given threshold. A review by Rubino & McCarthy [2] explored dendroecological methods used for the detection of historical disturbance events. Since then, several limitations of these methods have been discovered and additional criteria have been developed [3,4].

Tree-ring research frequently focuses on remnants of natural forests. Such studies typically identify canopy disturbances following windbreak [5] or extreme climatic events, such as drought [6]. Forest management is an equally important factor responsible for changes in tree-rings [7]. Coniferous and broad-leaved tree species positively respond to thinning or logging, which was demonstrated in several papers from North America [8–10]. Although the effects of recent canopy cutting on stem increment have often been studied, inferences about past management based on tree-rings are comparatively rare [11]. In Europe, various forms of woodland management have been practised for many centuries. The two most important management forms were coppicing and wood-pasture [12]. Coppicing can be traced in dendroarchaeological sources in prehistory [13] as well as in the Middle Ages [14]. Coppicing consisted of cutting trees close to the ground, letting them resprout from the cambium or dormant buds, and cutting the shoots repeatedly at short intervals. Combined with the coppice underwood, trees of generative origin (so-called standards) formed a characteristic feature of most coppices (Figure 1). In coppices-with-standards, the long-lived standards formed a scattered canopy over the short-rotation underwood. The density of standards was highly variable between sites and periods [15,16]. Standards were usually oaks, but other species also occurred [16]. Coppice woods experienced periodic shifts of insolation. A coppicing event was followed by a few years of increased solar radiation to soil surface [17]. Soil warmed up faster, microbial activity was higher, litter decomposed quicker and nutrients were available in larger amounts. Periodically improved light and nutrient conditions are supposed to have had an immediate effect on the growth of standard trees, which can be detected as abnormally increased increment in their annual rings [18].

Coppicing was gradually abandoned in North-Western and Central Europe by the mid-20th century, and the remaining few sites were retained for conservation purposes [18,19]. Reports about the last regular coppicing are usually from the second half of the 20th century [20,21]. The abandonment of coppicing has had a significant impact on forest biodiversity [22–27]. Succession from open-canopy forests and forests with frequent alterations of light and dark phases (typical for coppicing) resulted in the decline of entire herb layer communities and species [25] as well as critically endangered invertebrates [28]. The abandonment of coppicing has had a negative effect on some tree species as well. Oaks have gradually lost their ability to successfully regenerate in many European woodlands. This phenomenon is often referred to as 'oak decline' [29–31]. Available studies attribute it to various factors [32,33], e.g. plant diseases (e.g. *Microsphaera alphitoides*, *Phytophthora species*). Light availability is of particular importance in oak regeneration [34–37]. Due to low cutting intensity and subsequent competitive exclusion by shade-tolerant species [38,39] oak is becoming unable to reach the mature phase. The frequent recurrence of light pulses in coppices may have conditioned the successful regeneration of oak and may have thus influenced the long-term survival of this species. In active coppice woods, light phases are followed by periods of increased competition for light. Throughout their lifetime, long-lived oak standards experience several cycles of light and dark phases, which is reflected in tree-ring increment. Information gained from tree-ring data can be compared to archival forestry management documents. Such research provides a fine example of the combination of the methods of ecology and history for solving common research questions [40]. Knowledge about the legacy of historical management in coppices-with-standards can contribute to detecting the causes of oak decline in European woodlands.

Figure 1. Typical oak standard with a large straight stem and spreading branches in an abandoned coppice-with-standards. Photo by R. Hédl.
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There exist only a handful studies dealing with the effects of coppicing on tree-ring release in oak standards. Jones [41] quoted Bartet [42], who noticed significant release right after coppicing. However, in only one out of six English woods [18,43,44] did standards show a clear release following coppicing. None of the four coppicing events after the 1940s was responsible for anomalies in tree-ring growth in the Bradfield Woods in Sussex, and at only one of four sites on the western fringes of London (Mad Bess Wood) did trees demonstrate release due to recent coppicing. In the Bradfield Woods, there was great variation in tree-ring growth between the cored standards, thus no evidence for the effect of coppicing on standards could be provided. This scarcity of information about tree growth dynamics in coppices-with-standards sharply contrasts with the relatively abundant knowledge on forest dynamics based on tree-rings in other forest types.

In this paper, we focused on detecting the effects of historical coppicing on the growth dynamics of oak standards in a former coppice-with-standards in Central Europe. Our aims were 1) to relate the releases detected in tree-rings of oak standards to historical coppicing events, 2) to assess the intensity of competition of neighbouring trees with oak standards, and 3) to search for possible connections between oak regeneration patterns and historical coppicing events.

Methods

Study site

The study area is located in Děvín Wood (48°52′N, 16°39′E), in the Pálava Protected Landscape Area, Czech Republic (Figure 2). Pálava is an ancient cultural landscape situated in the north-western edge of the Pannonian Basin with relatively warm and dry subcontinental climate. Děvín forms a conspicuous limestone crest in a gently undulating landscape, with altitudes ranging from 260 to 549 m a.s.l. Soil types are mainly weakly eluviated luvisols and leptosols (rendzinas) rich in carbonates with topsoil pH (water) from ca. 6 to 8, and fertile mull humus forms [45]. Děvín covers 381 ha, of which 262 ha are wooded mainly by thermo- to mesophilous oak-hornbeam woodland (*Carpinion*).

Děvín Wood was intensively managed for centuries. The oldest written evidence about traditional management is from the 14th century and describes coppicing [15]. The cutting cycle gradually lengthened from the medieval 7 years to more than 30 years in the 19th century. Scattered among coppice stools, there was a historically fluctuating density of standard trees, mainly oaks [15]. In the second half of the 20th century, coppicing was abandoned in favour of high-forests and non-intervention conservation management. In 1946, a nature reserve was established at the site. Attempts to transform coppices to high-forests have lead

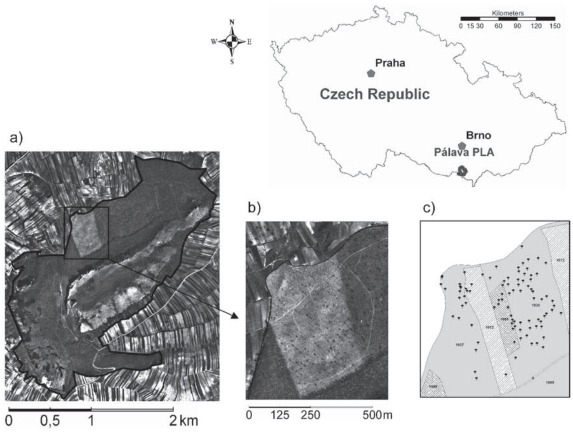

Figure 2. Location of the study site. The aerial photograph of Děvín Wood from 1938 (Military Geographical and Hydrometerological Office, Dobruška) depicts the last coppicing (a). The sample area (b) is visible as lighter rectangle with darker dots representing oak standards. c) shows the cored oak standards. The date of the last harvest is marked in each forest compartment.
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to the singling-out of many coppice stools. Singling-out means selecting the strongest adult shoot on each stool and cutting the rest of the stems, thus forming a pseudo-high-forest. Stools were singled out several times in the second half of the 20th century, e.g. in the 1970s and the 1990s. Today, the forest consists of high-forests, singled-out coppices with occasional old stools, and overgrown coppices. In many parts of the Wood the original standards are still clearly recognizable by their straight stems and characteristic branch architecture (Figure 1).

Sample area

The coring of oak standards took place in the area of the last regular coppicing in Děvín Wood. The coppiced part (24 ha) is apparent on an aerial photograph from 1938 as a lighter rectangle with standards as darker dots (Figure 2). It includes the adjacent parts of two forest compartments. Compartments had relatively stable boundaries throughout the centuries and usually coincided with the extent of historical coppicing events. In the central part of the sample area, there were two clear-cuts (1971 and 1990), removing most of the surviving standards. In addition to these systematic thinning events, occasional cutting occurred from the 1970s to the 1990s.

The only detailed historical record describing standards (rather than underwood) in Děvín Wood comes from 1808 (Moravský zemský archiv/Moravian Archives F72 inv. č. 3041). In this survey, standards were counted and recorded separately for each species and compartment. Standards in the sample area were composed of hornbeam (*Carpinus betulus*) (48%), oak (*Quercus petraea*) (29%), ash (*Fraxinus excelsior*) (12%) and lime (*Tilia platyphyllos*) (10%), with 48 standards per hectare. The density of standards in 1938 (determined by counting them in the freshly coppiced area on the 1938 aerial photograph) was much lower – only 10 standards per hectare, i.e. one fifth of the 1808 value. The density of standards in 2011 was 6 standards per hectare.

Data collection and analysis

Ninety stems of *Quercus petraea* agg. standards were cored in the winters of 2009–2011 and their exact geographical positions were recorded using differential GPS Trimble PathFinder Pro XRS. They represented all oak standards surviving in the sample area. Less frequent species, mainly *Carpinus betulus*, were omitted. Coring was carried out at a height of 1.3 m above ground surface, using a steel borer (Mora, Sweden). All cores were dried, mounted, sanded, and inspected for injuries, reaction wood and other aberrant features. Rings were counted from pith to bark and their widths measured to the nearest 0.01 mm using the TimeTable measuring device and PAST4 software (http://www.sciem.com). Ring-sequences were cross-dated visually using the pattern of wide and narrow rings, and verified using the program PAST4. A mean annual tree-ring width chronology was constructed and periods of oak establishment were determined on the basis of tree-rings.

To study neighbour effect on tree growth, all trees (3789 stems) with DBH >10 cm to a distance of 10 m around target oak standards were recorded. We opted for a distance of 10 m, because competition among trees is the most significant within this distance [46–49]. For each trunk we recorded the species, health status (living or dead), stem structure (multi-stemmed or single-stemmed) and measured the basal area of individual coppice stools.

Historical analysis of forest management

The recent history of coppicing in the study area was established based on archival sources. Seven sets of forest management plans (FMP) from 1883 to 1971 were used with their corresponding maps although unfortunately not all maps survived (Moravský zemský archiv/Moravian Archives F72 inv. č. 3044, kniha 113 and 116, F121 kniha 5 and 31 and Ústav pro hospodářskou úpravu lesů/Forest Management Institute, Brno, Czech Republic arch. č. 16/34). The FMPs recorded the age of each compartment, from which the date of coppicing events could be calculated. The maps were georeferenced, vectorized, and completed with information from the FMPs using ArcGIS software. It is to be noted that extracting dates of coppicing from FMPs is not entirely straightforward: coppicing was done in the autumn/winter season, but FMPs were connected to calendar years. In addition, it is known that some parts of stands were sometimes cut in two consecutive years, but we do not know the spatial details. Possible distortions were taken into consideration in the analyses by employing a 3-year tolerance margin.

Detection of release events

Release events were determined by *boundary line criteria* developed by Black & Abrams [3], who improved the formula of Nowacki & Abrams [11]. This method computes the percentage growth change (*%GC*) between average radial growth over the preceding 10-year period, M_1 (including the target year), and average radial growth over the subsequent 10-year period, M_2 (excluding the target year): $\%GC = [(M_2 - M_1)/M_1] * 100$. After this, the prior growth for each tree-ring (a mean of radial growth over the 10-year period before the target year) was calculated. The boundary line was constructed by dividing prior growth data into 0.5 mm segments and the top ten values of %GC were averaged within each segment. Finally, linear, power, logarithmic, and exponential curves were fitted to all positive segment averages and the function with the highest R^2 was selected. The resulting equation determines the boundary line. Growth change values between 20% and 49.9% of the boundary line were identified as moderate releases and those between 50% and 100% as major releases [3].

The boundary line was calculated using datasets from 12 sessile oak chronologies from the ITRDB (International Tree Ring Database) [50] and one chronology from the study of Dolezal et al. [29] (Table S1). Calculations were done in the programme R [51] by the script for release detection [52] and the Dendrochronology Program Library (dplR) [53]. The dates of coppicing events extracted from FMPs were compared to the releases detected by the tree-ring analyses.

Post-coppicing comparison of size and radial growth patterns between differently aged oak standards

To assess the growth pattern of oak standards in the past 50 years (after coppicing was abandoned in Děvín Wood), we compared the relative growth rate (RGR), cumulative stem diameter growth curves and resulting stem diameter structure for three groups of oak standards established before 1886, between 1886–1930, and after 1930. We also tested whether younger oak standards grew disproportionately more than older trees by relating the growth interval common for all trees for which information on growth history (tree-ring increments) was available (1953–2003) to prior stem size and age (1952). Finally, we assessed whether the three groups of trees that regenerated in different time periods preceding or following known coppicing events differ in various measures of crowding intensity from regenerating neighbouring trees (see next subchapter). Statistical differences in mean values of selected parameters were tested by analysis of variance.

Analysis of neighbour effect on tree growth

Whether trees in the close vicinity of oak standards had any effect on the radial growth increment of the standards was evaluated by relating both diameter increment (DI, linear one-dimensional measure) and basal area increment (BAI) to several indices of local competition (CI, or index of crowding intensity) using linear regression. As the response variables, DI and BAI, were highly correlated with each other (r = 0.98), we present only results using the first measure of radial growth. To assess the influence of neighbours on target tree growth (relative growth rates calculated as $RGR = [\ln(y_{i+1}) - \ln(y_1)]/yr$, where y_{i+1} is final stem diameter, y_1 is initial diameter, and yr is the length of the growth period in years), several CIs were calculated for each tree for which information on growth history was available to account for size-related neighbour effects, and for intraspecific vs. interspecific interference [54]. CIs were calculated as (1) the sum of individual basal areas of all neighbours within a circle of 10 m radius around the target stem, (2) the sum of stem basal areas of individual species, and (3) the sum of individual species stem basal areas divided into distinct categories based on health status (living or dead) and stem structure (multi-stemmed or single-stemmed, the latter representing singled-out coppice stools). Given the relatively low density of standard trees and because we do not assume any significant regeneration from seeds, most, if not all, neighbouring trees have resprouted from coppice stools. The neighbour effect of each CI was first analysed by a univariate regression model and analysis of variance to compare the strength of competition between the three groups of trees that regenerated in different time periods preceding or following known coppicing events.

Furthermore, to take into account the possible interaction between individual predictors, we modelled the neighbourhood effects of all CI indices using conditional inference trees (CIT, a type of classification and regression tree). This method belongs to non-parametric regressions that display a binary tree built by a process of recursive partitioning. CIT have been shown to give results that are comparable to those of traditional regression trees, but without their failings (overfitting and a biased selection of covariates when forming splits) [54]. CIT use a permutation-based statistical framework to ensure an even-handed selection of covariates and to stop splits being formed if they are not significant at some pre-specified level of significance (we used the 5% level of significance). The P-values were adjusted for multiple testing using the Bonferroni correction. The analysis was performed with the Party 1.0-3 package [55] in the R 2.13.1 program [51].

To evaluate possible temporal changes in competitive interactions during stand development following the last coppicing events, we included dead trees (visible as stump remnants) into the neighbourhood analyses. Such trees can play a significant role in competition in the early stages of stand development following coppicing. By analyzing simultaneously the effects of dead and living trees, we tested the prediction that a temporal shift took place in the mode of interaction from severe competition in the early phases of stand development resulting in tree mortality to more or less stable conditions following stand self-thinning. The neighbourhood analysis was conducted for a longer growth interval covering the entire post-cutting period 1953–2003, during which most oak standards showed a decline in radial growth resulting from decreasing light availability. To assess whether neighbour effect on tree growth changed over this period, we conducted complementary analyses for the separate intervals of 1953–1972 and 1973–2003.

Results

Coppicing and radial growth of oak standards

The average age of oak standards was 106 years and ranged from 28 years to 146 years. The first boundary line for *Quercus petraea* was computed on the basis of 45,755 tree-rings from 366 trees. The boundary line was fitted by an exponential function with the equation $y = 5.0067\, e^{-0.664x}$, which had the highest R^2 of 0.93. We identified altogether 126 releases (35 moderate, 91 major) across all tree-rings. The average number of release events per tree was 1.4.

A disturbance chronology was constructed for the period from 1890 to 1999 for 5-year segments. Releases occurred with four exceptions in all 22 segments and the percentage of trees showing release varied substantially. However, large peaks in disturbance events were detected for the periods 1895–1899 and 1935–1939 (Figure 3a). A higher proportion of disturbance events was identified also in the second half of 1970s and the first half of 1990s, but these events were not as pronounced as the previous ones (Figure 3a). Mean annual tree-ring width chronology showed highest values in the years 1897 and 1939 after abrupt increases in growth (Figure 4). The boundary line method detected two major releases for the mean chronology in the years 1895 and 1935 (Figure 4). We observed abnormally high average tree-ring growth for a 22-year period following both coppicing events. These periods were statistically significantly different from other periods (Tukey's HSD Post-hoc test, $P<0.01$, Figure 5).

Releases detected by tree-ring analysis were related to historical records of coppice events. According to the FMPs, the analysed compartments were coppiced in 1895–1897 and in 1935–1937. Parts of the sample area were felled in the 1970s (25% of the area) and the 1990s (6%), related to attempts to transform the coppice-with-standards to high-forest. Twenty-six trees experienced both historical coppicing events. Over 90% of the detected releases could be matched with historical coppicing events within a 3-year tolerance limit, which was introduced because of the inaccuracies inherent archival sources. Further releases were detected in the second half of the 1970s and the first half of the 1990s when coppice management already ceased. The number of these releases was relatively small compared to those following coppicing events. Unfortunately it was not possible to locate these recent events precisely in space and match them with individual trees, because cutting was scattered.

Comparison of size and radial growth parameters between differently aged oak standards after the abandonment of coppicing

When oak standards established before 1886, in the period 1886–1930 and after 1930 were compared in terms of radial growth, size parameters and cumulative increment curves, those established after 1930 had significantly higher RGR in the period 1952–2003 (ANOVA, $P=0.023$, Figure 6), and were still growing actively with no sign of growth decline (no apparent asymptote) (Figure 7). Despite higher relative increments, trees established after 1930 still had a significantly smaller stem diameter in 2003

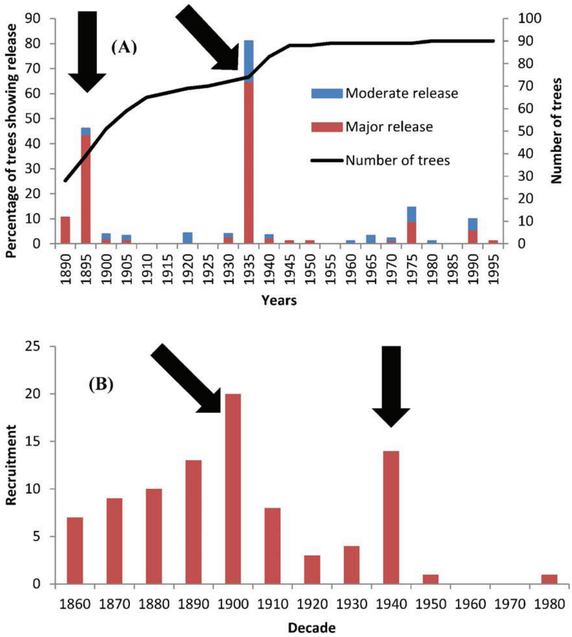

Figure 3. (A) Percentage of trees showing release in 5-year intervals, as identified with the boundary-line release criteria. The two main releases closely followed coppicing events. Releases in the 1970s and 1990s coincide with the major singling-out of coppice stools. (B) Number of trees established in individual decades (age was determined on the basis of increment cores taken at breast height). With two exceptions, all oak standards originated before or shortly after the last regular coppicing in 1935/1937. The two main coppicing events are indicated by black arrows.
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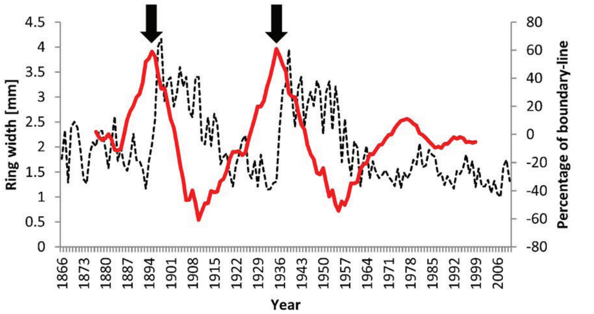

Figure 4. The average annual radial growth of *Q. petraea* standards (dashed line) and values of boundary-line for this mean growth (red line). The two main coppicing events are indicated by black arrows.
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(P = 0.012, Figure 6) than asymptotically-growing older oak standards that showed a decline in radial growth after 1950. Size- and age-growth regressions (Figure 8 a, b) revealed that the diameter increment of oak standards from 1953 to 2003 was negatively correlated with stem diameter and tree age in 1952, indicating that younger oak standards grew disproportionately more than older conspecifics. This is likely to have been caused by recently reduced competition. Neighbouring stems around younger standards are significantly less dense and have lower basal area ($P<0.05$, Figure 6).

Neighbour effect on the growth of oak standards

On average 43.5 stems (31% dead and 69% living) were recorded around target oak standards to a distance of 10 m. The majority of neighbouring stems (86%) had a multi-stemmed structure, which proves that they had originated from coppice stools. The most abundant species in the vicinity of oak standards was *Tilia platyphyllos* (2435 stems) making up 64% of the total number of neighbours (1501 living stems and 851 dead stems were coppice shoots, and 83 stems were living single-stemmed trees), followed by *Carpinus betulus* (572 stems, of which 259 were coppice shoots), conspecific oaks (356 stems, mostly living) and *Fraxinus excelsior* (231 stems, mostly living). The remaining 15% were *Acer campestre*, *Acer pseudoplatanus*, *Acer platanoides*, *Ulmus minor*, *Populus tremula*, *Cerasus avium*, *Sorbus torminalis*, *Cornus mas*, *Betula pendula* and *Castanea sativa*. Among these, only *Acer campestre* had more than one percent (60 stems) of the total number of neighbouring stems.

The competition indices that were significantly negatively correlated with the diameter increments incorporated mainly interspecific effects of *Tilia platyphyllos* living and dead trees (Figure 8 c, d). The growth reductions of oak standards due to competition from other tree species were non-significant. Explained variance (adjusted r^2) from the significant univariate regressions of RGR of oak from 1953 to 2003 on those competition indices ranged from 4.3% to 13.7%, and it increased mostly when dead *Tilia* individuals were used to define a local neighbourhood. In fact, the single competition index that accounted for the most variation was based solely on basal areas

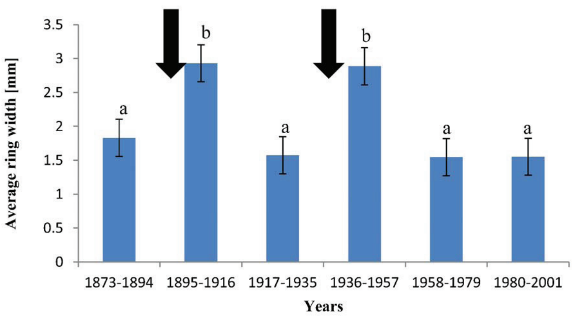

Figure 5. Average tree-ring growth for 22-year time periods. Arrows mark the last two historical coppicing events. The periods after coppicing had significantly higher average tree-ring increments than the periods not following coppice events. Columns sharing the same letter are not significantly different at $p<0.01$ (ANOVA followed by Tukey's HSD post-hoc tests). Error bars represent standard error. The period 1917–1935 includes a 19-year time span, because there are no more years before the first coppicing event (1935).
doi:10.1371/journal.pone.0055770.g005

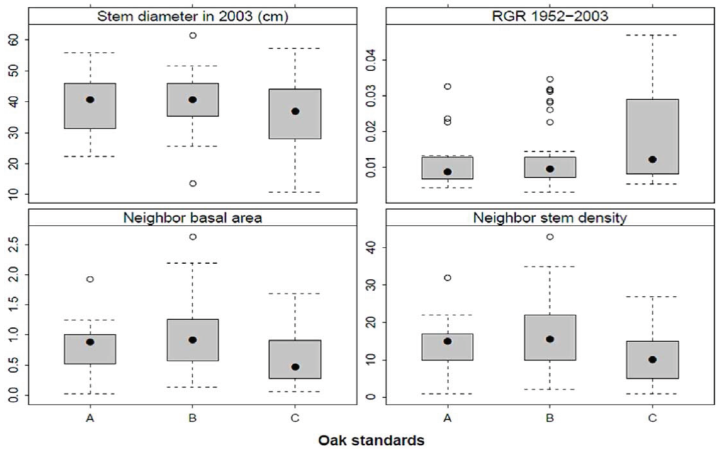

Figure 6. Comparison of stem diameter, relative growth rate (RGR) and competition indices (sum of basal area of all living and dead neighbours, and the density of dead neighbouring stems) of oaks established before 1886 (A), between 1886 and 1930 (B), and after 1930 (C). Boxes represent 25–75% of values, black dots medians, whiskers 1.5 interquartile ranges, and open dots outliers.
doi:10.1371/journal.pone.0055770.g006

of multi-stemmed *Tilia* trees (adjusted $r^2 = 0.073$, $P = 0.02$). The separate analyses for the two periods 1953–1972 and 1973–2003 revealed a stronger competitive effect of neighbouring trees for the first period 1953–1972, when *Tilia* neighbours explained 13.5% variability in radial growth increments compared to 9.3% variability explained in the second period. Permutation-based conditional inference trees (CIT) supported the results of univariate regressions, showing primarily the effect of dead and living *Tilia platyphyllos* trees on the growth reduction of oak standards.

Relationship between coppicing and oak regeneration

The rate of recruitment of trees established between 1860 and 1899 (64% of cored oaks) was relatively even, as opposed to those

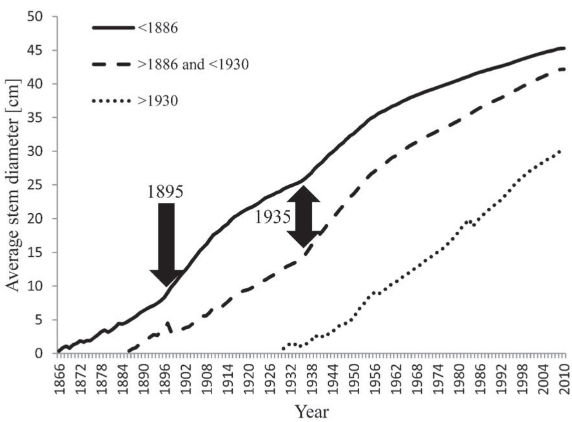

Figure 7. Mean cumulative stem diameter growth curves for three groups of oak standards established before 1886, between 1886 and 1930, and after 1930 with respect to the two coppicing events (marked by thick arrows).
doi:10.1371/journal.pone.0055770.g007

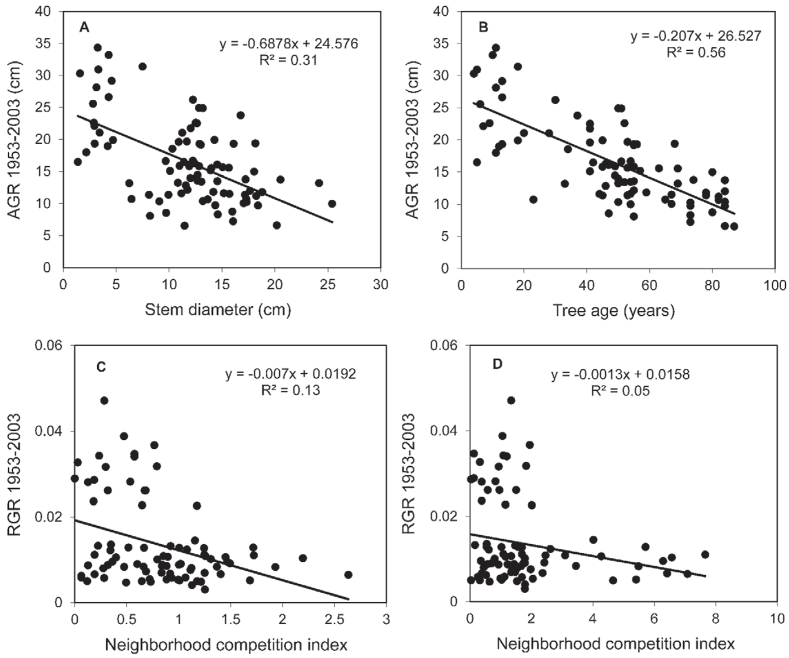

Figure 8. Relationships between: (a) diameter increment from 1953 to 2003 (AGR, absolute growth rate) and stem diameter in 1952; (b) AGR and tree age in 1952; (c, d) relative growth rate (RGR) of diameter increment and the intensity of neighbourhood competition (crowding) within 10 m; where in (c) basal areas (in m^2) of all dead trees were considered, while in (d) *Tilia platyphyllos* living and dead trees were analysed.
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established in the 20th century (Figure 3b). After coppicing events, the number of trees that survived from establishment grew markedly. Most of the surviving trees were from the decades following coppice events - 20 trees (22% of cored oaks) established during the decade after the 1896–7 coppicing event and 14 trees (16%) after the 1935–7 coppicing event have survived until the present, while for other decades the average is 5 trees (Figure 3b).

Discussion

Effects of coppicing on the growth of oak standards

In Děvín Wood, the periods of enhanced radial growth of standard trees started with pronounced peaks and lasted for about two decades before levelling to normal values. We were able to match these events with the dates of known coppicing events, hence providing unique evidence for past coppicing in the radial growth of standard trees. Percentage change in radial growth allowed us to distinguish severe (major release) disturbance events from mild (moderate release) events [3]. We identified a much higher proportion of major releases than of moderate ones due to coppicing. From an ecological perspective, coppicing at our study site can therefore be considered as a severe disturbance event. Dendrochronological methods used for disturbance analysis are based on the change of light availability for surviving trees after disturbance events [3,11,56]. Light pulses following coppicing were probably the main factor inducing abrupt growth changes in standards.

Explaining the effects of coppicing

It seems that the increase in radial growth in standard oaks after coppicing is controlled by the intensity of competition with underwood. This competition is temporarily abolished or lowered after coppicing, enabling standards to grow beyond their usual increment. This effect gradually declines as the resprouting underwood regains the space between standards. The period of increased growth after coppicing in Děvín Wood was much more longer (22 years) than the period documented in other studies, which ranged from 6 years [57] through 7–12 years [58] to 15 years [59]. The site-specific setting of environmental conditions, stem density, species composition and the size of the gaps may lead to contrasting patterns [11], which probably applies to the reaction of standards to coppicing as well. Competition for light is negligible when the underwood is too small to compete for light with the protruding standards. However, as the coppicing cycle lengthened to several decades, competition for light could have had a significant effect. The same is true for young standards before they reach the canopy and are not shaded anymore. Nevertheless, there can also be other factors influencing radial growth.

The increased availability of soil nutrients after removing the dense underwood (usually in winter months) can be important at nutrient-poor sites. According to this view, increased solar radiation in early spring enhances soil microbial activity [18], mobilizing soil nitrogen that can be utilized by standards to jump-increase their radial growth. However, in Děvín Wood the substrate is exceptionally fertile. Soils are deep loamy-clayey slope accumulations with a high pH (6–8 in water) and a mull type of humus indicating very fast litter decomposition. These soils are rich in organic matter, nitrogen and base cations, providing sufficient nutrients [45].

Another factor responsible for coppicing-related releases in Děvín Wood could be competition for water. The site has relatively warm and dry climate and soil water is deficient. In the vegetation season from April to September, precipitation is only 367 mm and average temperature 16.1°C (Mikulov and Perná, data for 1947–1978, Czech Hydrometeorological Institute). Periods of drought occur frequently posing the most important constraint for plant growth. Consequently, temporary reduction of competition for water might have triggered the abnormal tree-ring increments following coppicing events in Děvín Wood. By contrast, no soil water limitations may have caused the failure to detect coppicing at English sites [18,43].

Growth of standards is influenced by neighbouring trees

We found that the species composition of competing underwood can be an important factor for the growth of standards. Over 95% of *Tilia* in Děvín Wood is *T. platyphyllos* [60]. It resprouts from coppice stools in large numbers at the site. A typical multi-stemmed stool of *Tilia* has ca. 10, sometimes up to 20 shoots (H. Malíková, unpublished data). Because the oak standards were taller than resprouting *Tilia*, competition for light is not the sole explanation for the effect *Tilia* had on the growth of standards. We suggest that this effect was also driven by competition for soil resources because *T. platyphyllos* develops very dense roots in the topsoil in order to satisfy its exceptionally high demands for water, and sustain its relatively high concentration of nutrients in leaves [61,62]. Dense coppice shoots of *T. platyphyllos* were a major competitor for light and soil resources to the surrounding trees including oak standards in the early stages of stand development following coppicing. The neighbourhood analyses demonstrated the negative effects of neighbours (mainly former underwood trees) on stem diameter increment of oak standards in 1953–2003. The neighbourhood model fitted best when the neighbouring trees of *Tilia* were included, while other tree species including conspecific neighbours had a minor impact. This supports the assumption of non-equivalent neighbour effects [63]. The strongest growth reduction in oak standards was explained by dead *Tilia* trees, i.e. remnants of coppice stools included in the mapping of neighbouring trees in 2012. These *Tilia* trees were probably established after the last coppicing and perished gradually through competition. This process slowly improved growth conditions for oak standards. Standards exhibited a stronger negative effect during the first 20–40 years following the last major coppicing event in the 1930s than in later periods.

Oak decline and management history

Information about newly established oak standards completes our knowledge about the performance of oak standards. Standard dendrochronological methods cannot reconstruct the processes of the early stages of tree development. On the basis of our results, we cannot directly infer the reasons for the oak decline [29,30], because our analysis involved only relatively old oak individuals. However, the establishment of new oak standards clearly followed the coppicing events. The analysis of oak recruitment in Děvín Wood revealed a significant increase in the number of trees established after both coppicing events, and virtually no recruitment in the decades after the 1940s, when the site became a reserve with restricted management. At other sites, this synchronous trend between tree recruitment and disturbance events was documented primarily after large natural disturbances [64–67] but also after harvesting [65,68]. The analysis of 206 vegetation plots sampled in Děvín Wood in 2002–2003 [60] showed that oak seedlings occurred only rarely. Currently, oak does not regenerate in Děvín Wood at all. The last significant regeneration of oaks that subsequently reached the phase of mature trees had been in the 1940s, following the last regular coppicing.

Oak seedlings perform better under high insolation than other dominant tree species, such as beech [69,70]. Oak cannot stand competition with shade-casting and shade-tolerant tree species in the long run [39]. Under unfavourable conditions, most oak seedlings grow for about five years and subsequently die if light conditions do not improve [71]. In forest environments, favourable conditions for successful oak regeneration include open canopy [37,38] and non-shading understorey vegetation [72]. Although it is not clear how open forests could have been maintained in prehistory [73], coppice management was certainly capable of creating suitable conditions for oak regeneration in the past millennium [15,16]. Human influence through management is therefore likely to have contributed to the long-term presence of oak in European woodlands.. In today's shady, closed-canopy European forests, opening up the canopy may be the only possible way for oaks to reach maturity.

Supporting Information

Table S1 Tree-ring data sources used in the development of boundary-line and absolute increase threshold (ITRDB = International Tree Ring Database).
(DOCX)

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Author Contributions

Conceived and designed the experiments: JA RH PS JD. Performed the experiments: JA RH PS PM VR JM MK JD. Analyzed the data: JA JD PS JM. Wrote the paper: JA RH PS JM MK JD.

References

1. Frelich LE (2002) Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests: Cambridge University Press.
2. Rubino DL, McCarthy BC (2004) Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia 21: 97–115.
3. Black BA, Abrams MD (2003) Use of boundary-line growth patterns as a basis for dendroecological release criteria. Ecol Appl 13: 1733–1749.
4. Fraver S, White AS (2005) Identifying growth releases in dendrochronological studies of forest disturbance. Can J Forest Res 35: 1648–1656.5.

5. Altman J, Doležal J, Černý T, Song J-S (2012) Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings. Glob Change Biol. DOI: 10.1111/gcb.12067
6. Williams AP, Allen CD, Millar CI, Swetnam TW, Michaelsen J, et al. (2010) Forest responses to increasing aridity and warmth in the southwestern United States. P Natl Academy USA 107: 21289–21294.
7. Spiecker H (2002) Tree rings and forest management in Europe. Dendrochronologia 20: 191–202.
8. Oliver WW (1986) Growth of California red fir advance regeneration after overstory removal and thinning. USDA For Serv PSW R: 180.
9. Zhang JW, Oliver WW (2006) Stand structure and growth of Abies magnifica responded to five thinning levels in northeastern California, USA. Forest Ecol Manag 223: 275–283.
10. Webster CR, Jensen NR (2007) A shift in the gap dynamics of Betula alleghaniensis in response to single-tree selection. Can J Forest Res 37: 682–689.
11. Nowacki GJ, Abrams MD (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecol Monogr 67: 225–249.
12. Bergmeier E, Petermann J, Schroder E (2010) Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. Biodivers Conserv 19: 2995–3014.
13. Billamboz A (2003) Tree Rings and Wetland Occupation in Southwest Germany Between 2000 and 500 Bc: Dendroarchaeology Beyond Dating in Tribute to F. H. Schweingruber: Tree-Ring Society.
14. Haneca K, Boeren I, Van Acker J, Beeckman H (2006) Dendrochronology in suboptimal conditions: tree rings from medieval oak from Flanders (Belgium) as dating tools and archives of past forest management. Veg Hist Archaeobot 15: 137–144.
15. Szabo P (2010) Driving forces of stability and change in woodland structure: A case-study from the Czech lowlands. Forest Ecol Manag 259: 650–656.
16. Rackham O (2003) Ancient Woodland: Its History, Vegetation and Uses in England. Colvend: Castlepoint Press. 624 p.
17. Mitchell PL, Woodward FI (1987) Instrument for measuring temperature, photosynthetically active radiation and daylength, and its use in the measurement of daylength and tempeture in coppice. J Appl Ecol 24: 239–249.
18. Bridge MC, Hibbert FA, Rackham O (1986) Effects of coppicing on the growth of oak timber trees in the Bradfield Woods, Suffolk. J Ecol 74: 1095–1102.
19. Fuller R, Peterken G (1995) Woodland and scrub. In: Sutherland W, Hill D, editors. Managing habitats for conservation. Cambridge, UK: Cambridge University Press. pp. 327–361.
20. Caquet B, Montpied P, Dreyer E, Epron D, Collet C (2010) Response to canopy opening does not act as a filter to Fagus sylvatica and Acer sp advance regeneration in a mixed temperate forest. Ann For Sci 67.
21. Nunez V, Hernando A, Velazquez J, Tejera R (2012) Livestock management in Natura 2000: A case study in a Quercus pyrenaica neglected coppice forest. J Nat Conserv 20: 1–9.
22. Ito H, Hino T, Sakuma D (2012) Species abundance in floor vegetation of managed coppice and abandoned forest. Forest Ecol Manag 269: 99–105.
23. Yamaura Y, Royle JA, Shimada N, Asanuma S, Sato T, et al. (2012) Biodiversity of man-made open habitats in an underused country: a class of multispecies abundance models for count data. Biodivers Conserv 21: 1365–1380.
24. Broome A, Clarke S, Peace A, Parsons M (2011) The effect of coppice management on moth assemblages in an English woodland. Biodivers Conserv 20: 729–749.
25. Hedl R, Kopecky M, Komarek J (2010) Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Divers Distrib 16: 267–276.
26. Baeten L, Bauwens B, De Schrijver A, De Keersmaeker L, Van Calster H, et al. (2009) Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. Appl Veg Sci 12: 187–197.
27. Kopecký M, Hédl R, Szabó P (2012) Non-random extinctions dominate plant community changes in abandoned coppices. J Appl Ecol. DOI: 10.1111/1365-2664.12010.
28. Konvicka M, Cizek O, Filipova L, Fric Z, Benes J, et al. (2005) For whom the bells toll: Demography of the last population of the butterfly Euphydryas maturna in the Czech Republic. Biologia 60: 551–557.
29. Helama S, Laanelaid A, Raisio J, Tuomenvirta H (2009) Oak decline in Helsinki portrayed by tree-rings, climate and soil data. Plant Soil 319: 163–174.
30. Dolezal J, Mazurek P, Klimesova J (2010) Oak decline in southern Moravia: the association between climate change and early and late wood formation in oaks. Preslia 82: 289–306.
31. Gomez-Aparicio L, Perez-Ramos IM, Mendoza I, Matias L, Quero JL, et al. (2008) Oak seedling survival and growth along resource gradients in Mediterranean forests: implications for regeneration in current and future environmental scenarios. Oikos 117: 1683–1699.
32. Luisi N, Lerario P, Vannini A (1993) Recent Advances in Studies on Oak Decline: Proceedings of an International Congress, Selva Di Fasano (Brindisi), Italy, September 13–18, 1992: Dipartimento di Patologia Vegetale, Università degli Studi.
33. Jung T, Blaschke H, Osswald W (2000) Involvement of soilborne Phytophthora species in Central European oak decline and the effect of site factors on the disease. Plant Pathol 49: 706–718.
34. Emborg J (1998) Understorey light conditions and regeneration with respect to the structural dynamics of a near-natural temperate deciduous forest in Denmark. Forest Ecol Manag 106: 83–95.
35. Kelly DL (2002) The regeneration of Quercus petraea (sessile oak) in southwest Ireland: a 25-year experimental study. Forest Ecol Manag 166: 207–226.
36. Iverson LR, Hutchinson TF, Prasad AM, Peters MP (2008) Thinning, fire, and oak regeneration across a heterogeneous landscape in the eastern US: 7-year results. Forest Ecol Manag 255: 3035–3050.
37. von Lupke B (1998) Silvicultural methods of oak regeneration with special respect to shade tolerant mixed species. Forest Ecol Manag 106: 19–26.
38. Dobrowolska D (2008) Effect of stand density on oak regeneration in flood plain forests in Lower Silesia, Poland. Forestry 81: 511–523.
39. Collet C, Piboule A, Leroy O, Frochot H (2008) Advance Fagus sylvatica and Acer pseudoplatanus seedlings dominate tree regeneration in a mixed broad-leaved former coppice-with-standards forest. Forestry 81: 135–150.
40. Szabo P, Hedl R (2011) Advancing the Integration of History and Ecology for Conservation. Conserv Biol 25: 680–687.
41. Jones EW (1959) Biological flora of the British-Isles Quercus L. J Ecol 47: 169–222.
42. Bartet E (1890) Influence excercée par l'époque de l'abattage sur la production et le développelent des rejets des souches dans les taillis. Rev Eaux Forests 29: 310–313.
43. Bridge MC, Winchester V (2000) An evaluation of standard oak tree growth in Ruislip woods, West London. Bot J Linn Soc 134: 61–71.
44. Rackham O (1975) Hayley Wood: Its History and Ecology: Cambridgeshire and Isle of Ely Naturalists' Trust.
45. Hedl R, Rejsek K (2007) Soil changes after forty years of succession in an abandoned coppice in the Czech Republic. Acta Agron Hung 55: 453–474.
46. Condit R, Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, et al. (2000) Spatial patterns in the distribution of tropical tree species. Science 288: 1414–1418.
47. Zhang J, Song B, Li BH, Ye J, Wang XG, et al. (2010) Spatial patterns and associations of six congeneric species in an old-growth temperate forest. Acta Oecol 36: 29–38.
48. Olano JM, Laskurain NA, Escudero A, De La Cruz M (2009) Why and where do adult trees die in a young secondary temperate forest? The role of neighbourhood. Ann For Sci 66: 8.
49. Cartanson M, Floret C, Galan MJ, Grandjanny M, Lefloch E, et al. (1992) Factors affecting radial growth of *Quercus ilex* L. in a coppice stand in southern. Vegetatio 100: 61–68.
50. NOAA (2012) Contributors of the International Tree-Ring Data Bank, IGBP PAGES/World Data Center for Paleoclimatology, NOAA/NGDC Paleoclimatology Program. Boulder, Colorado, , USA.
51. R Development Core Team (2011) R: A language and environment for statistical computing, version 2.13.1. R Foundation for Statistical Computing, Vienna, Austria.
52. Aakala T, Kuuluvainen T, Wallenius T, Kauhanen H (2011) Tree mortality episodes in the intact Picea abies-dominated taiga in the Arkhangelsk region of northern European Russia. J Veg Sci 22: 322–333.
53. Bunn AG (2008) A dendrochronology program library in R (dplR). Dendrochronologia 26: 115–124.
54. Dolezal J, Ishii H, Vetrova VP, Sumida A, Hara T (2004) Tree growth and competition in a Betula platyphylla-Larix cajanderi post-fire forest in central Kamchatka. Ann Bot 94: 333–343.
55. Hothorn T, Hornik K, Zeileis A (2006) Unbiased recursive partitioning: A conditional inference framework. J Comput Graph Stat 15: 651–674.
56. Lorimer CG, Frelich LE (1989) A methodology for estimating canopy disturbance frequency and intensity in dense temperate forests. Can J Forest Res 19: 651–663.
57. Hilt DE (1979) Diameter growth of upland oaks after thinning. USDA For Serv NE RES:437.
58. Rentch JS, Desta F, Miller GW (2002) Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, USA. Can J Forest Res 32: 915–927.
59. Erdmann GG, Oberg RR (1973) Fifteen-year results from six cutting methods in second-growth northern hardwoods. USDA For Serv NC R P:100.
60. Hedl R (2005) Srovnání stavu lesních ekosystémů NPR Děvín po 50 letech přirozené sukcese. Brno: Mendelova zemědělská a lesnická univerzita.
61. Holscher D, Hertel D, Leuschner C, Hottkowitz M (2002) Tree species diversity and soil patchiness in a temperate broad-leaved forest with limited rooting space. Flora 197: 118–125.
62. Holscher D, Schmitt S, Kupfer K (2002) Growth and leaf traits of four broad-leaved tree species along a hillside gradient. Forstwiss Centralbl 121: 229–239.
63. Dolezal J, Song JS, Altman J, Janecek S, Cerny T, et al. (2009) Tree growth and competition in a post-logging Quercus mongolica forest on Mt. Sobaek, South Korea. Ecol Res 24: 281–290.
64. Fraver S, White AS, Seymour RS (2009) Natural disturbance in an old-growth landscape of northern Maine, USA. J Ecol 97: 289–298.
65. Busby PE, Canham CD, Motzkin G, Foster DR (2009) Forest response to chronic hurricane disturbance in coastal New England. J Veg Sci 20: 487–497.
66. Svoboda M, Janda P, Nagel TA, Fraver S, Rejzek J, et al. (2012) Disturbance history of an old-growth sub-alpine *Picea abies* stand in the Bohemian Forest, Czech Republic. J Veg Sci 23: 86–97.

67. Splechtna BE, Gratzer G, Black BA (2005) Disturbance history of a European old-growth mixed-species forest - A spatial dendro-ecological analysis. J Veg Sci 16: 511–522.
68. Swaine MD, Agyeman VK (2008) Enhanced tree recruitment following logging in two forest reserves in Ghana. Biotropica 40: 370–374.
69. Welander NT, Ottosson B (1998) The influence of shading on growth and morphology in seedlings of *Quercus robur* L. and *Fagus sylvatica* L. Forest Ecol Manag 107: 117–126.
70. Valladares F, Chico JM, Aranda I, Balaguer L, Dizengremel P, et al. (2002) The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. Trees-Struct Funct 16: 395–403.
71. Lorimer CG, Chapman JW, Lambert WD (1994) Tall uderstorey vegetation as a factor in the poor development of oak seedlings beneath mature stands. J Ecol 82: 227–237.
72. Harmer R, Morgan G (2007) Development of Quercus robur advance regeneration following canopy reduction in an oak woodland. Forestry 80: 137–149.
73. Birks HJB (2005) Mind the gap: how open were European primeval forests? Trends Ecol Evol 20: 154–156.

Chapter IV

Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings

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Photo on previous page: leaves of Mongolian oak (*Quercus mongolica*).

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Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings

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Abstract

The globally observed trend of changing intensity of tropical cyclones over the past few decades emphasizes the need for a better understanding of the effects of such disturbance events in natural and inhabited areas. On the Korean Peninsula, typhoon intensity has increased over the past 100 years as evidenced by instrumental data recorded from 1904 until present. We examined how the increase in three weather characteristics (maximum hourly and daily precipitation, and maximum wind speed) during the typhoon activity affected old-growth oak forests. *Quercus mongolica* is a dominant species in the Korean mountains and the growth releases from 220 individuals from three sites along a latitudinal gradient (33–38°N) of decreasing typhoon activity were studied. Growth releases indicate tree-stand disturbance and improved light conditions for surviving trees. The trends in release events corresponded to spatiotemporal gradients in maximum wind speed and precipitation. A high positive correlation was found between the maximum values of typhoon characteristics and the proportion of trees showing release. A higher proportion of disturbed trees was found in the middle and southern parts of the Korean peninsula where typhoons are most intense. This shows that the releases are associated with typhoons and also indicates the differential impact of typhoons on the forests. Finally, we present a record of the changing proportion of trees showing release based on tree-rings for the period 1770–1979. The reconstruction revealed no trend during the period 1770–1879, while the rate of forest disturbances increased rapidly from 1880 to 1979. Our results suggest that if typhoon intensity rises, as is projected by some climatic models, the number of forest disturbance events will increase thus altering the disturbance regime and ecosystem processes.

Keywords: boundary line, climate change, forest disturbance, *Quercus mongolica*, tree-ring, typhoon

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Introduction

Tropical cyclones are one of the most common hazards facing people around the world and the increasing impact of such disturbances on ecosystems is predicted as climate change progress (Lugo, 2000; Dale *et al.*, 2001). Recent studies documented an increase in distribution, frequency, extent, and intensity of different kinds of disturbance, for example: fire (Williams *et al.*, 2010), windstorms (Etkin, 1995), and landslides (Buma & Dehn, 1998). Recent tropical cyclones (i.e., hurricanes in the north Atlantic Ocean and the northeast Pacific Ocean or typhoons in the northwest Pacific Ocean) have also been more frequent and intense than before (Goldenberg *et al.*, 2001; Webster *et al.*, 2005; Santer *et al.*, 2006; Vecchi *et al.*, 2008; Bender *et al.*, 2010), and several have had a significant social and economic impact (Pielke *et al.*, 2008). The effects and outcomes of increasing frequency and intensity of hurricanes on forest ecosystems were summarized by Lugo (2000). On the other hand, there are studies which do not support these conclusions about increasing wind disturbance (Klotzbach, 2006; Vecchi & Knutson, 2008).

Old-growth forest ecosystems offer one of the best opportunities for studying disturbances in nature (Fraver *et al.*, 2009) because their longevity enables us to reconstruct historical disturbance regimes. However, old-growth forests free from human activity are rather rare in the temperate regions of the northern hemisphere (Peterken, 1996). Until now, most of our knowledge about the influence of disturbances on forest stands was derived from studies in North America and Europe, whereas Asia remains less explored. The Korean peninsula, a region with frequent typhoons, is particularly suitable for exploring and supplementing our current knowledge of disturbance effects on forests. Research in this area is very important for understanding how disturbance processes influence the dynamics of forests having

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the highest plant diversity in the temperate zone and how these processes are changing in time.

Typhoons affecting the Korean peninsula arise in the Philippine Sea and move northwest, where they gradually lose power or turn towards the northeast. This process makes the Korean peninsula a unique place for exploring the impact of typhoons on forests along the gradient of decreasing typhoon frequency from the south to north. For research on disturbance processes across a large area, it is acceptable to study a single widespread species. In our study region, the Mongolian oak (*Quercus mongolica*) is such a candidate as it occurs in Korea and throughout temperate forest areas across NE China, the Russian Far East, and northern Japan (Krestov *et al*., 2006).

Our objective in this study was to determine the forest site disturbance history for *Q. mongolica* trees using dendroecological methods. Specifically, we aimed to (1) assess how typhoon frequency and intensity have changed in the long-term, (2) explore differences in frequency of release events along latitudinal gradients of decreasing typhoon intensity, (3) analyse how individual characteristics of typhoons affect the frequency of release events, and (4) reconstruct frequency of release events in the past 200 years.

Materials and methods

Study area

Our study sites were located in the three mountainous regions (Hallasan, Jirisan, Seoraksan) placed along the latitudinal gradient (33–38°N) in South Korea (Fig. 1). Owing to the high population density and historical background, most of this area is covered by secondary woodlands from low to middle elevations. Natural old-growth forests are therefore to be found only in large mountain areas, where logging is affected by terrain restrictions and these areas are now protected by National Park status. The selected stands were natural, old-growth deciduous forests, which had not been subjected to major disturbances in the last two decades (e.g., as indicated by the absence of groups of fallen logs and large gaps).

Mean annual air temperature for the Seoraksan mountains (northern part of the study region) is 11.2 °C, with the mean for January −3.2 °C and for July 23.9 °C; the mean annual precipitation is around 1237 mm. For the Jeju Island (Hallasan), the southernmost part, the mean annual temperature is 15.7 °C, with the mean January temperature being 5.8 °C and the mean July temperature 26.7 °C. The mean annual precipitation rises from about 1500 mm in coastal areas to over 4500 mm in upland areas (averages for the period 1971–2000). January receives the lowest and July the highest amount of rainfall in Korea. The climate on the Korean peninsula is strongly influenced by cold air masses from Siberia in winter and monsoons and tropical storms or typhoons from the north part of the Pacific Ocean in summer.

Data collection and analysis

During the summers of 2005, 2006, and 2007 we set up twenty-one 20 × 20 m permanent plots (seven in each mountain region) located within the forest stands dominated by *Q. mongolica*. We collected core samples from all stems (>10 cm DBH) of *Q. mongolica* growing inside each 20 × 20 m permanent plot at a height of 0.5–1 m above the ground surface using a steel borer (Mora, Sweden). All cores were dried, mounted, sanded, and inspected for injuries, reaction wood, and other aberrant features. Rings were counted from pith to bark and their widths measured to the nearest 0.01 mm using the TimeTable measuring device and PAST4 software (http://www.sciem.com). Ring-sequences were cross-dated visually using the pattern of wide and narrow rings, and verified using the PAST4 program by percentage of parallel variation (*Gleichläufigkeit*), which is based on counting how well the growth curves followed the same trend in growth changes (Eckstein & Bauch, 1969). In total, we measured and analysed 30 036 tree-rings from 220 trees. Increment cores used for reconstruction of the disturbance history were taken from 156 old-growth trees (Seoraksan – 63, Jirisan – 44, Hallasan – 49). Another 64 young oaks (<50 years old) from our study of secondary forests (Dolezal *et al*., 2009) were added to better

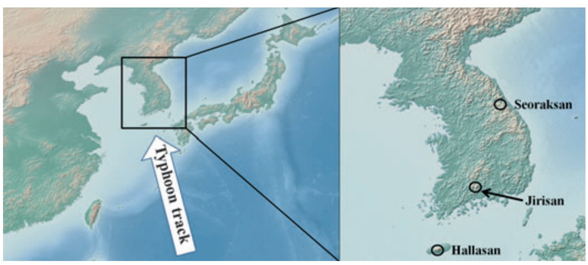

Fig. 1 Location of Korean peninsula in E Asia with illustration of path of typhoons affecting Korean peninsula (left side). Site locations on southern part of Korean peninsula (right side).

determine the boundary line (Black & Abrams, 2003). The oldest tree extends back to 1651 AD.

The release events were determined by boundary line criteria (Black & Abrams, 2003), which improve the formula of Nowacki & Abrams (1997). Growth change values between 20% and 49.9% of the boundary line were identified as moderate releases and those between 50% and 100% as major releases. Calculations were done in program R (R Development Core Team, 2011) by the script for release detection (Aakala *et al*., 2011) and the Dendrochronology Program Library in R (dplR) (Bunn, 2008). We first combined the growth release data from all three study areas together to assess the general pattern of forest disturbance from 1770 to 1979. The period before 1770 was not included because of the small number (<10) of trees. The decades after 1970 with a low proportion of trees showing release were also removed; our stands were selected to be in a time period with no evidence of recent disturbance. We then developed a master tree-ring chronology for each site using a conservative detrending of ring-width series with a negative exponential function in program R (R Development Core Team, 2011) by employing the dplR (Bunn, 2008). To capture changes in stand-level growth and disturbances, we show the temporal course of ring-width index of mean standardized chronology (RWI) together with release numbers on an annual timescale.

To determine whether or not the detected growth releases were associated with canopy disturbance and hence improved light conditions due to severe wind disturbances, we gathered the meteorological data about the occurrence of typhoons on the southern part of the Korean peninsula for the period 1904–2008 from the Typhoon White Book (Korea Meteorological Administration, 2011). These data were measured in 49 meteorological stations placed equally along the latitudinal gradient in South Korea. For each individual typhoon, we extracted information about the date that it arose, maximum wind speed, and hourly and daily maximum precipitation. We also extracted information about typhoons from stations surrounding our study sites for comparison with these localities. Comparison of the proportion of trees showing release and typhoon intensity between national parks was tested using one-way ANOVA with Tukey *post hoc* tests in program R (R Development Core Team, 2011). We made an analysis comparing the mean release magnitude with typhoon magnitude via regression. We made this analysis only for Jirisan NP, because the dataset of maximum wind speed is from the year 1954 without absenting values for individual years (for the two other localities, data from surrounding meteorological stations are scattered). We used correlation and regression analyses to assess how individual climatic attributes correlated with the number of typhoons in individual years, and if there were some detectable trends over the 20th century.

Results

The average number of typhoons affecting the study area in the period 1904–2008 was 3.1 per year and only 4 years were without typhoons. The number of typhoons was closely related to individual climatic parameters and correlated positively with the maximum hourly (Fig. 2) and daily precipitation ($R = 0.28$ and $R = 0.25$ respectively; $P < 0.05$) (Supplementary Figure S1a). The highest correlation coefficient was found between the number of typhoons and the maximum wind speed ($R = 0.30$; $P < 0.05$) (Supplementary Figure S1b). All three characteristics showed an increasing trend from 1904 until 2008.

In total, we measured more than 30 000 tree-rings. The mean values of Gleichläufigkeit for individual sites are sufficient for the verification of cross-dating (65% for Hallasan, 67.2% for Jirisan, and 64.6% for Seoraksan; $P < 0.05$). From the 156 individuals finally used in this analysis (sample depth for individual sites is shown in Supplementary Figure S2a–c), 70% ($n = 109$) showed at least one release event throughout their life. The results were obtained by application of the boundary line (Black & Abrams, 2003) fitted to ring-width data by a logarithmic function with the equation $y = 195.73 - 153.9\ln(x)$, which had the highest R^2 of 0.986.

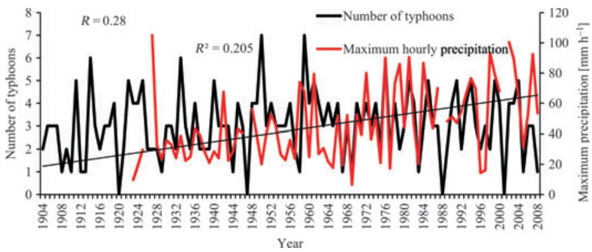

Fig. 2 Number of typhoons over Korea (black line) and maximum hourly precipitation (red line) for individual years during the typhoon activity. Linear regression for maximum hourly precipitation during typhoon activity is shown. *R*, correlation coefficient between typhoon frequency and individual typhoon characteristics; R^2, coefficient of determination of individual linear regressions.

Maximum wind speed showed significant differences between the southern and northern parts as well as between and middle and northern parts (Fig. 3a). Comparison of the percentage of trees showing release between the southern (Hallasan), middle (Jirisan), and northern (Seoraksan) parts of South Korea (Fig. 3b) revealed significant differences between the southern and northern parts. Hallasan showed the highest occurrence (80%) of trees which showed release events. Jirisan, situated roughly in the middle of our investigated area, had 72% of trunks which had some release events. Finally, in Seoraksan mountains we identified 62% of trees in which at least one disturbance was detected.

The RWI and detected releases on an annual timescale showed that a rise in the master chronology was usually preceded by multiple disturbances and these were preceded by strong typhoon(s) at all three sites (Supplementary Figure S3a–c). The regression analysis showed that with increasing maximum wind speed there was also an increase in the mean value of the boundary line, but with a 2-year delay ($P < 0.05$) (Supplementary Figure S4). We found that major releases followed the most intensive typhoons (measured by the maximum daily precipitation) and they were always accompanied by a high number of moderate releases (within a 2-year tolerance) (Table 1).

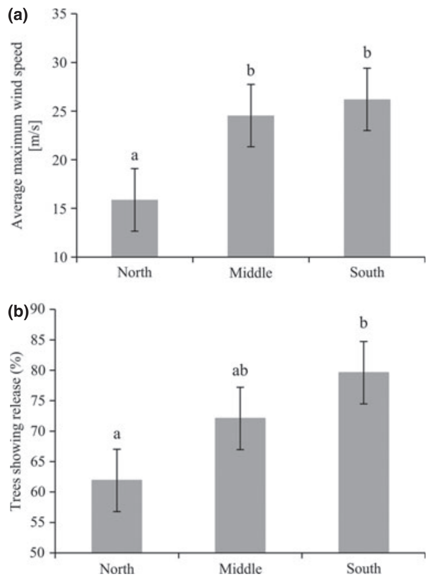

Fig. 3 Differences in (a) average maximum wind speed and (b) percentage of trees showing release in our study locations (North = Seoraksan mountains, Middle = Jirisan mountains, and South = Hallasan mountains). Columns sharing the same letter are not significantly different at $P < 0.05$ (ANOVA followed by Tukey *post hoc* tests). Error bars represent standard error.

We combined the growth release data from all three study areas to assess whether or not the occurrence of detected releases is related to climatic data during the typhoons. The maximum values of the three climatic characteristics of typhoons per decade were strongly correlated with the proportion of trees showing release during the same decade. A strong relationship was found for maximum daily precipitation ($R = 0.74$; $P < 0.05$) (Fig. 4), maximum hourly precipitation ($R = 0.90$; $P < 0.05$) (Supplementary Figure S5a), and maximum wind speed ($R = 0.55$; nonsignificant) (Supplementary Figure S5b).

Finally, we present a record of the changing proportion of trees showing release based on tree-rings for the period 1770–1979. The disturbance chronology represented by the proportion of trees showing release has two different phases (Fig. 5). The first one is from 1770 to 1879 and in this period there was no noticeable trend. The period from 1880 to 1979, however, provided evidence of an increasing proportion of trees showing release. This increasing trend was found also when we analysed all three sites separately (Supplementary Figure S6a–c).

Discussion

Using meteorological data, we examined changes in the basic weather characteristics of typhoons in the 20th century. We only analysed datasets as a whole and we did not make a separate analysis for each site. The reasons for this were the fact that typhoons affected large areas and that data from all meteorological stations represented a longer and more robust dataset and mirrored common trends better. Not surprisingly, we found a relatively high correlation between investigated typhoon characteristics and typhoon frequency. We also found an increasing trend of maximum precipitation over the period from 1904 to 2008 and also of maximum wind speed (1938–2008) during typhoon activity. These findings are not completely new and were documented in a few recent studies (Oouchi *et al.*, 2006; Kim & Jain, 2011). However, the length of the dataset is several decades longer in comparison with published climatological studies, which run from 1970 to the present time (Wu *et al.*, 2005; Tu *et al.*, 2009; Kim & Jain, 2011; Park *et al.*, 2011). These results are thus essential for understanding exactly what affects the ecosystems throughout typhoons. An increase in the

Table 1 Comparison of number of releases (moderate and major), number (percentage) of moderate releases associated with major releases for individual sites, and maximum daily precipitation [mm per day] for typhoons in the years with major releases and in the other years. In the brackets below name of study site is time span for which meteorological information was available

	Number of detected releases		Moderate releases associated with major releases	Maximum daily precipitation [mm per day] for typhoons in the years with	
	Moderate	Major		Major releases	Other years
Seoraksan (1914–1979)	37	14	28 (76%)	180.1	117.2
Jirisan (1904–1979)	35	8	27 (77%)	175.5	69.7
Hallasan (1923–1979)	26	19	22 (85%)	202.2	95.1

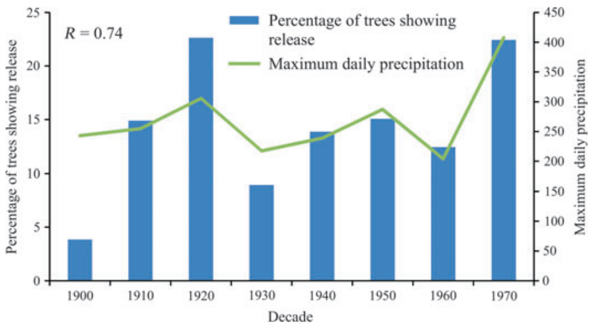

Fig. 4 Percentage of trees showing release (blue columns) and maximum daily precipitation; green line) for individual decades. *R*, correlation coefficient between proportion of trees showing release and maximum daily precipitation during typhoon activity ($P < 0.05$).

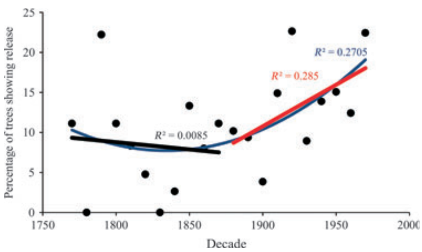

Fig. 5 Disturbance chronology demonstrating the distribution of trees showing release. Lines represented the trend for given time span (black line = 1770–1879; red line = 1880–1979) and R^2, coefficient of determination for these trends.

amount of precipitation during the 20th century was globally observed at approximately by 0.98% per decade (New *et al.*, 2001) and tree-ring reconstruction in Eurasia indicates a large-scale trend towards pluvial conditions in the 20th century (Treydte *et al.*, 2006). On the other hand, in certain parts of the globe such as the western United States and central Europe, there is a recent trend towards drier conditions (Cook *et al.*, 2004; Dolezal *et al.*, 2010; Williams *et al.*, 2010).

On the basis of our results, we can observe differences in the ratio of trees along latitudinal gradients where growth was affected by disturbances. Typhoon activity decreases from south to north in our area (Wang & Qian, 2005), just as the percentage of trees showing disturbances does. Typhoon intensity expressed by maximum wind speed also decreases from the south to the north. This indicates that areas with a higher occurrence of typhoons have a higher proportion of trees which experienced disturbance. This is direct evidence connecting the frequency and rate of disturbances, or more precisely release events. To our knowledge, there are no comparative data from other parts of the world showing the proportion of disturbances along tropical cyclone gradients. A few studies examined if the frequency of cyclones affected forest structure, specifically the height of trees in Africa (de Gouvenain & Silander, 2003), East Asia (Lin *et al.*, 2003), and America (Brokaw *et al.*, 2004). All of these have shown that in areas with frequent strong winds, trees are shorter than those outside the cyclone range (Lugo, 2008).

We found a close relationship between the intensity of typhoons and the proportion of trees showing release but not between the number of typhoons and the proportion of releases. This indicates that the frequency of typhoons is not the main factor affecting the forest structure. The dominant agent seems to be, as expected, typhoon intensity. Although in these times of climatic change there is debate on whether the frequency of typhoons is changing, the increasing intensity of cyclones seems to be clear.

As far as we know, this is the first study which connects climatic data and the detection of disturbances using tree-rings; there is a real lack of data connecting these two issues. Previous studies are focused on very intense cyclones (Boucher *et al.*, 1990; Kupfer *et al.*, 2008) and do not explore the effects of all possible factors affecting forest structure in the past, the main reason for this is the scarcity of additional information related to observed cyclones in most regions of the world (Lugo, 2008). Surprisingly, we found the weakest relationship between the proportion of trees showing release and wind velocity; this can be deduced from different aspects of our plots. Some of the stands are located on leeward sides or protected by a landscape barrier. The other reason is the short period of wind velocity records and hence the low number of degrees of freedom in the analysis. On the other hand, correlation between the proportion of trees showing release and maximum precipitation is very strong. The reason could be that the mountains explored in this study have a relatively low elevation for creating a rain shadow effect. Therefore, the amount of precipitation will be more evenly distributed between sites when compared with wind speed, which can vary considerably and in a stochastic way. For this reason, maximum precipitation seems to be a better characteristic of typhoon strength over the larger area. Our findings confirmed this: major releases occurred only around the years with higher maximum precipitation during typhoon intensity and were accompanied by a higher proportion of moderate releases.

Our release event reconstruction over two centuries (1770–1970) reveals an increasing trend in the proportion of trees showing release from the end of 19th century. These findings correspond with the increasing number of tropical cyclones documented in last decades and, primarily, with their increasing destructiveness (Emanuel, 2005; Webster *et al.*, 2005). The resulting destructive effects in these cases are mainly associated with the trend of increased wind speed and amount of precipitation. We can certainly exclude the effects of human disturbances during the 20th century. Study sites were situated in the higher parts of mountains in old-growth forests (with trees older than 150 years and no sign of logging), whereas logging was carried out in the lower parts of our sites or in lower, flatter, and better accessible mountains in Korea (Dolezal *et al.*, 2009, 2012).

As mentioned above, most of the climatological studies from our area only considered a relatively short period (1970 to the present time). These observations are actually at the end of the period over which we can compare the release rate of stands (due to the constraints of the method used). In view of the fact that we found a high correlation between intense typhoons and the rate of releases, there is no reason to suspect a different relationship in subsequent years. The long-term climatological observations of typhoon weather characteristics used in this and other studies confirmed the increasing trend in typhoon intensity over the last decades. Predictions for the next century are for a further similar increase in typhoon intensity (Esteban *et al.*, 2010). On the basis of our tree-ring analysis we suggest that the increasing effect of cyclones will not only be restricted to East Asia but everywhere affected by them. These further changes will particularly affect densely populated areas such as Korea, Japan, Taiwan or the eastern coast of China. These areas will be forced to adapt to these changes.

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References

Aakala T, Kuuluvainen T, Wallenius T, Kauhanen H (2011) Tree mortality episodes in the intact Picea abies-dominated taiga in the Arkhangelsk region of northern European Russia. *Journal of Vegetation Science*, **22**, 322–333.

Bender MA, Knutson TR, Tuleya RE, Sirutis JJ, Vecchi GA, Garner ST, Held IM (2010) Modeled impact of anthropogenic warming on the frequency of intense Atlantic Hurricanes. *Science*, **327**, 454–458.

Black BA, Abrams MD (2003) Use of boundary-line growth patterns as a basis for dendroecological release criteria. *Ecological Applications*, **13**, 1733–1749.

Boucher DH, Vandermeer JH, Yih K, Zamora N (1990) Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology*, **71**, 2022–2024.

Brokaw N, Fraver S, Grear JS *et al.* (2004) Disturbance and canopy structure in two tropical forests. In: *Tropical Forest Diversity and Dynamism: Findings from a*

Large-Scale Plot Network (eds Losos E, Leigh EG Jr), pp. 177–194. The University of Chicago Press, Chicago.

Buma J, Dehn M (1998) A method for predicting the impact of climate change on slope stability. *Environmental Geology*, **35**, 190–196.

Bunn AG (2008) A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**, 115–124.

Cook ER, Woodhouse CA, Eakin CM, Meko DM, Stahle DW (2004) Long-term aridity changes in the western United States. *Science*, **306**, 1015–1018.

Dale VH, Joyce LA, McNulty S *et al*. (2001) Climate change and forest disturbances. *BioScience*, **51**, 723–734.

Dolezal J, Song JS, Altman J, Janecek S, Cerny T, Srutek M, Kolbek J (2009) Tree growth and competition in a post-logging *Quercus mongolica* forest on Mt. Sobaek, South Korea. *Ecological Research*, **24**, 281–290.

Dolezal J, Mazurek P, Klimesova J (2010) Oak decline in southern Moravia: the association between climate change and early and late wood formation in oaks. *Preslia*, **82**, 289–306.

Dolezal J, Altman J, Kopecky M *et al*. (2012) Plant diversity changes during the postglacial in East Asia: insights from forest refugia on Halla Volcano, Jeju Island. *PLoS ONE*, **7**, e33065.

Eckstein D, Bauch J (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. *Forstwissenschaftliches Centralblatt*, **88**, 230–250.

Emanuel K (2005) Increasing destructiveness of tropical cyclones over the past 30 years. *Nature*, **436**, 686–688.

Esteban M, Webersik C, Shibayama T (2010) Methodology for the estimation of the increase in time loss due to future increase in tropical cyclone intensity in Japan. *Climatic Change*, **102**, 555–578.

Etkin DA (1995) Beyond the year 2000, more tornadoes in western Canada? Implications from the historical record. *Natural Hazards*, **12**, 19–27.

Fraver S, White AS, Seymour RS (2009) Natural disturbance in an old-growth landscape of northern Maine, USA. *Journal of Ecology*, **97**, 289–298.

Goldenberg SB, Landsea CW, Mestas-Nunez AM, Gray WM (2001) The recent increase in Atlantic hurricane activity: causes and implications. *Science*, **293**, 474–479.

de Gouvenain RC, Silander JA (2003) Do tropical storm regimes influence the structure of tropical lowland rain forests? *Biotropica*, **35**, 166–180.

Kim JS, Jain S (2011) Precipitation trends over the Korean peninsula: typhoon-induced changes and a typology for characterizing climate-related risk. *Environmental Research Letters*, **6**, 034033.

Klotzbach PJ (2006) Trends in global tropical cyclone activity over the past twenty years (1986–2005). *Geophysical Research Letters*, **33**, L10805.

Korea Meteorological Administration (2011) *Typhoon White Book*. National typhoon center, Jeju.

Krestov PV, Song JS, Nakamura Y, Verkholat VP (2006) A phytosociological survey of the deciduous temperate forests of mainland Northeast Asia. *Phytocoenologia*, **36**, 77–150.

Kupfer JA, Myers AT, McLane SE, Melton GN (2008) Patterns of forest damage in a southern Mississippi landscape caused by Hurricane Katrina. *Ecosystems*, **11**, 45–60.

Lin KC, Hamburg SP, Tang S, Hsia YJ, Lin TC (2003) Typhoon effects on litterfall in a subtropical forest. *Canadian Journal of Forest Research*, **33**, 2184–2192.

Lugo AE (2000) Effects and outcomes of Caribbean hurricanes in a climate change scenario. *Science of the Total Environment*, **262**, 243–251.

Lugo AE (2008) Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology*, **33**, 368–398.

New M, Todd M, Hulme M, Jones P (2001) Precipitation measurements and trends in the twentieth century. *International Journal of Climatology*, **21**, 1899–1922.

Nowacki GJ, Abrams MD (1997) Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecological Monographs*, **67**, 225–249.

Oouchi K, Yoshimura J, Yoshimura H, Mizuta R, Kusunoki S, Noda A (2006) Tropical cyclone climatology in a global-warming climate as simulated in a 20 km-mesh global atmospheric model: frequency and wind intensity analyses. *Journal of the Meteorological Society of Japan*, **84**, 259–276.

Park DSR, Ho CH, Kim JH, Kim HS (2011) Strong landfall typhoons in Korea and Japan in a recent decade. *Journal of Geophysical Research-Atmospheres*, **116**, D07105.

Peterken GF (1996) *Natural Woodland: Ecology and Conservation in Northern Temperate Regions*. Cambridge University Press, Cambridge, UK.

Pielke RA, Gratz J, Landsea CW, Collins D, Saunders MA, Musulin R (2008) Normalized hurricane damage in the United States: 1900–2005. *Natural Hazards Review*, **9**, 29–42.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing, version 2.13.1*. R Foundation for Statistical Computing, Vienna, Austria.

Santer BD, Wigley TML, Gleckler PJ *et al*. (2006) Forced and unforced ocean temperature changes in Atlantic and Pacific tropical cyclogenesis regions. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 13905–13910.

Treydte KS, Schleser GH, Helle G, Frank DC, Winiger M, Haug GH, Esper J (2006) The twentieth century was the wettest period in northern Pakistan over the past millennium. *Nature*, **440**, 1179–1182.

Tu JY, Chou C, Chu PS (2009) The abrupt shift of typhoon activity in the vicinity of Taiwan and its association with western north Pacific-East Asian climate change. *Journal of Climate*, **22**, 3617–3628.

Vecchi GA, Knutson TR (2008) On estimates of historical north Atlantic tropical cyclone activity. *Journal of Climate*, **21**, 3580–3600.

Vecchi GA, Swanson KL, Soden BJ (2008) Climate change whither hurricane activity? *Science*, **322**, 687–689.

Wang JB, Qian WH (2005) Statistic analysis of tropical cyclone impact on the China mainland during the last half century. *Chinese Journal of Geophysics-Chinese Edition*, **48**, 992–999.

Webster PJ, Holland GJ, Curry JA, Chang HR (2005) Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science*, **309**, 1844–1846.

Williams AP, Allen CD, Millar CI, Swetnam TW, Michaelsen J, Still CJ, Leavitt SW (2010) Forest responses to increasing aridity and warmth in the southwestern United States. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 21289–21294.

Wu LG, Wang B, Geng SQ (2005) Growing typhoon influence on east Asia. *Geophysical Research Letters*, **32**, L18703.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Number of typhoons over Korea (black lines) and (a) maximum daily precipitation, and (b) maximum wind speed (red lines) for individual years during the typhoon activity. Linear regressions for individual weather characteristics during typhoon activity are shown. *R*, correlation coefficient between typhoon frequency and individual typhoon characteristics; R^2, coefficient of determination of individual linear regressions.

Figure S2. Sample depth (=number of samples) for individual study areas (a) Hallasan, (b) Jirisan, and (c) Seoraksan mountains.

Figure S3. Relationship between RWI (grey line) with the smoothed values (10-year running mean; black line) and detected releases (columns) on an annual timescale for individual study areas (a) Hallasan, (b) Jirisan, and (c) Seoraksan mountains. Black arrows represent major typhoons in given period, with average maximum wind speed 39.3 [m s^{-1}] for Hallasan, 36.9 for Jirisan, and 15.7 for Seoraksan.

Figure S4. Positive relationship between maximum wind speed and mean value of boundary line ($P < 0.05$).

Figure S5. Relationship between percentage of trees showing release (blue columns) and (a) maximum hourly precipitation ($P < 0.05$), and (b) maximum wind speed (nonsignificant) represented by green lines. *R*, correlation coefficient between proportion of trees showing release and individual weather characteristics during typhoon activity.

Figure S6. Disturbance chronology demonstrating the distribution of trees showing release for the time span where the number of trees is >10. Increasing trend for release events from the end of the 19th century is shown for all sites. R^2, coefficient of determination for these trends.

Chapter V

Impact of severe tropical cyclones on forest over 230 years: spatiotemporal linking of past disturbances with frequency and diversity of tree establishment

Altman, J., Dolezal, J., Fibich, P., Leps, J., Uemura, S. & Hara, T. (2014) under review in Global Change Biology

Photo on previous page: a mixed temperate forest with dense understory bamboo, Hallasan Mountains, Jeju Island, South Korea.

Impact of severe tropical cyclones on forest over 230 years: spatiotemporal linking of past disturbances with frequency and diversity of tree establishment

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Abstract

The globally observed increase in intensity of tropical cyclones (i.e. hurricanes and typhoons) over the past few decades may disrupt the stability of natural ecosystems. In Eastern Asian forests, severe typhoons create large openings which allow invading understory bamboo to suppress other biota in the understory. Intermediate disturbances seem to support tree regeneration and coexistence. The current state of knowledge is derived from relatively short-term observations, but little is known about the long-term patterns and processes. In this study, the impact of severe and intermediate wind disturbances on tree recruitment and diversity in an oak-fir-maple forest over the 230 years was explored. Disturbances were reconstructed from 385 individual trees from 15 species by growth-release analysis. Altogether 310 major and 293 moderate releases were identified, indicating severe and intermediate tree disturbances. These were both temporally and spatially localized, with 80% of events detected in only four time periods: 1775-1784, 1815-1839, 1880-1909 and 1950-1979, followed by an elevated rate of tree establishment. Disturbances triggered a noticeable recruitment in the 1775-1814, 1900-1939, and 1955-1979 periods. Dendrochronological reconstruction showed that severe disturbances caused both large and small gaps. Spatial pattern analysis revealed that higher density and diversity of recruitment (altogether recorded 19 species) was associated mostly with small gaps and un-disturbed forest, while large gaps likely became overgrown by bamboo in place of tree recruitment. These results provide evidence that severe typhoons interacting with a strong biotic filter (understory bamboo) can disrupt forest ecosystems functioning by significantly reducing the extent and diversity of tree recruitment. These findings are especially important as most of the climate models predict an increasing intensity of tropical cyclones, which can affect an ecosystem's structure and diversity.

This part is the subject of unpublished manuscript. The full version of this part of Chapter V is archived by the Faculty of Science, University of South Bohemia in the printed version of the Ph.D. Thesis.

Chapter VI

Conclusions

Photo on previous page: a view of Jirisan Mountains, South Korea.

Conclusions

The main objective of this thesis is to contribute to the knowledge about disturbance detection by means of tree-ring analysis. Specifically, I focused on release detection, which provides non-direct evidence of past disturbances. Evidence is derived from both understory and overstory trees, which survived the disturbance. Such trees recorded the disturbance in the growth trend as an abrupt increase in growth after improved light conditions, which arise after death of the neighbouring tree(s) (i.e. a release).

The research work that is presented in this thesis at first aimed to give a basic background, review of current knowledge about methods used for release detection, their strengths, limitations and future challenges (Chapter I). Moreover, a universal tool for release detection, the TRADER package, was presented (Chapter II). Furthermore, this dissertation demonstrated the successful application of methods for release detection on various ecological aspects concerning forest management, long-term changes in natural forest ecosystems, forest diversity and the impact of global changes (Chapter III-V).

It is documented in the literature, and also in this thesis, that release detection methods, despite their inherent uncertainties, can be widely used for disturbance reconstruction with promising results. On the basis of the review presented here it can be concluded that: 1) a 10-year window for calculating growth change seems to be the best option; 2) 25% and 50% minimum thresholds for detection moderate and major releases respectively seems to give good results for the radial growth averaging method; 3) regardless of the high number of methods, future research should be concentrated on these with broad applicability and their testing and development (Chapter I).

Calculation of growth change itself is not complicated and can be performed in commonly used spreadsheets. However the checking and processing of results or application of advanced methods (e.g. boundary-line) is already more complicated and time consuming without special tools. Surprisingly, no common tool existed for release detection analysis until recently. This lack lead to development of TRADER package in the open-source R environment. TRADER enables the disturbance reconstruction by a total of 24 published methods and functions for the detection of tree recruitment, and growth trends were also included. Furthermore, TRADER enables comparison between individual methods, which is easily achieved by making parameter changes and the clearly arranged graphical and tabular outputs (Chapter II).

Disturbance reconstruction frequently focuses on remnants of natural forests, however, forest management is an equally important factor responsible for changes in tree-rings. Therefore, we focused on detecting the effects of historical coppicing on the growth dynamics of oak standards in a former coppice-with-standards in Central Europe. Historical records of coppice events matched with large peaks in radial growth found for the periods 1895–1899 and 1935–1939. Moreover, past coppicing was followed by recruitment of oak standards which basically ceased after coppicing was abandoned in the second half of 20th century. Various competition indices revealed a negative effect of neighbouring trees on the growth of oak standards. On the basis of these results it can concluded that the conversion of coppicing to high-forest induced significant radial-growth decreases of economically interesting standards and also endangered forest regeneration for shade-intolerant species (Chapter III).

Changes in forest management practices are not the only ones which potentially endanger forest ecosystems and their dynamics. In times of global changes, shifts in frequency and intensity of natural disturbance agents to more frequent or more intense events occur. The area most affected by such changes is East Asia, where increases in typhoon intensity is described and the most evident increase is predicted (compared to other areas affected by tropical cyclones). In South Korea, we have an exceptional opportunity to compare long records of climate data with the release detection along latitudinal gradients. A very high positive correlation was found between reconstructed disturbances and weather characteristics of typhoons in 20th century. Reconstruction of past typhoon activity showed no trend during the period 1770–1879, while the rate of forest disturbances increased rapidly from 1880 to 1979 (Chapter IV).

Such rapid changes in forest disturbance dynamics can affect the long-term patterns and processes. To understand such changes in detail, the impact of severe and intermediate wind disturbances on tree recruitment and diversity in an oak-fir-maple forest over the 230 years was explored. The study site, Hokkaido Island, Japan, was at the edge of typhoon occurrence, which allowed detailed analysis of single disturbances, which would be impossible in more affected areas. The main findings were that forest regeneration is strongly connected to severe disturbances, which results in the creation of both large and small openings. The results of disturbance reconstruction were combined with spatial pattern analysis. Spatial-temporal analysis revealed that higher density and diversity of recruitment was associated mainly with un-disturbed forest and small gaps (trees with moderate release). On the contrary, large gaps suppress regeneration due to the development of an extremely dense bamboo understory. It is suggested here that the increasing intensity of tropical cyclones creates a higher number of large gaps at the expense smaller ones, which will affect forest structure and species diversity (Chapter V).

Curriculum Vitae

Name: Jan Altman

Born: 25th May 1985 in Cheb, Czechoslovakia

Education & Degrees:

2010 to date: Ph.D. study programme Botany, Faculty of Science, University of South Bohemia, České Budějovice

2007-2010: master's degree from Botany, Faculty of Biological Science, University of South Bohemia, České Budějovice, Czech Republic

2008-2009: master's degree from Ecosystem Biology, Faculty of Biological Science, University of South Bohemia, České Budějovice, Czech Republic

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2009 to date: Institute of Botany AS CR, Research Division Třeboň, Dept. of Ecology

Research interest:

Dendrochronology; disturbance analysis by the mean of tree-rings; global changes; forest management; structure, diversity and growth of the forests; herbochronology, drift-wood

Expeditions:

South Korea (2006, 2007, 2009, 2010, 2011, 2012) altogether more than 6 months

Cameroon (2007, 2012, 2013) altogether 4 months

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Research training:

2014 International Course on Wood Anatomy & Tree-Ring Ecology, České Budějovice, Czech Republic. Teachers: Gärtner H., Schweingruber F.H. & Crivellaro A.

2013 research fellowship in Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Birmensdorf, Switzerland. Collaboration with Treydte K., Schweingruber F.H. & Büntgen U.

2011 24th Dendroecological Fieldweek, Swiss Federal Institute for Forest, Snow and Landscape Research, WSL. Engelberg, Switzerland. Organizers: Treydte K. & Frank D.

Supervision and teaching:

Supervisor or co-supervisor of 10 bachelor or diploma thesis.

Partly teach: field seminar of Ecology; Forest ecology (lectures and field seminar); and Ecology of mountain ecosystems. Faculty of Science, University of South Bohemia.

Projects:

2014-2016: co-investigator of *"Effects of changing growth conditions on tree increment, stand production and vitality – danger or opportunity for the Central- European forestry"* funded by GA ČR (14-12262S).

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Conferences:

Hořák D., Janeček S., Sedláček O., Riegert J., Doležal J., Albrecht T., Bartoš M., Nana E.D., Dančák M., Tropek R., Padyšáková E., **Altman J**., Ferenc M. (2014) *Ten years of Czech ecological research in Cameroon*. Annual Conference of the Society for Tropical Ecology, 25-28 February, Freising, Germany. Poster presentation.

Altman J., Doležal J., Fibich P., Leps J., Hara T. (2014) *Forest response to different intensity of tropical cyclones: spatiotemporal linking of past disturbances with frequency and diversity of tree establishment*. WorldDendro 2014, 13-17 January, Melbourne, Australia. Oral presentation.

Altman J., Doležal J., Jánská E., Čížek L. (2014) *Tree responses to forest management changes: oak reaction on canopy closure and flood control system*. WorldDendro 2014, 13-17 January, Melbourne, Australia. Poster presentation.

Dolezal J., **Altman J**., Dancak M., Svoboda M., Schweingruber F. (2014) *Altitudinal changes in forest composition, structure and wood density on Mt. Cameroon, western Africa*. WorldDendro 2014, 13-17 January, Melbourne, Australia. Poster presentation.

Dolezal J., Schweingruber F., Riha P., Chlumska Z., **Altman J**. (2014) *Plant anatomical characters and their variation along environmental gradients: a key to understanding plant evolution, adaptation and function*. WorldDendro 2014, 13-17 January, Melbourne, Australia. Oral presentation.

Sebek P., **Altman J**., Platek M. & Cizek L (2013) *Pollarding as a management tool in the conservation of tree hollow fauna*. Intecol 2013, 18-23 August, London, UK. Oral presentation.

Hedl R., **Altman J**., Szabo P., Riedl V., Mazurek P., Mullerova J., Kopecky M., Dolezal J. (2012) *Tree-rings mirror the management legacy: growth and regeneration of oak standards in coppice woodlands*. BES 2012, 17-20 December, Birmingham, UK. Oral presentation.

Sebek P., **Altman J**., Platek M., Cizek L. (2012) *Pollarding as a tool for conservation of tree hollow fauna*. The 8th European Conference on Ecological Restoration, 9-14 September 2012, Ceske Budejovice, Czech republic. Oral presentation.

Altman J., Doležal J., Song J.S., Černý T., Šrůtek M. (2012) *Forest response to increasing typhoon activity on the Korean peninsula:*

evidence from oak tree-rings. TRACE 2012, 9-12 May, Potsdam, Germany. Poster presentation.

Altman J., Doležal J., Song J.S., Plener T., Pejcha V., Janeček Š., Černý T., Šrůtek M. (2011) *Dendroecological study of disturbances in Quercus mongolica forests in a landscape with frequent typhoons*. 19-23 September, EURODENDRO 2011, Engelberg, Switzerland. Poster presentation

Publications:

Černý T., Kopecký M., Petřík P., Song, J.S., Šrůtek M., Valachovič M., **Altman J**., Doležal J. (2014) Classification of Korean forests: patterns along geographic and environmental gradients. *Applied Vegetation Science*: DOI: 10.1111/avsc.12124

Altman J., Fibich P., Dolezal J. & Aakala T. (2014) TRADER: a package for Tree Ring Analysis of Disturbance Events in R. *Dendrochronologia*: 32, 107-112.

Doležal J., **Altman J**., Vetrova V.P. & Hara T. (2014) Linking two centuries of tree growth and glacier dynamics with climate changes in Kamchatka. *Climate Change* 124: 207-220.

Šebek P., **Altman J**., Plátek M. & Čížek L. (2013) Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. *PLoS ONE* 8(3): e60456.

Altman J., Hédl R., Szabó P., Mazůrek P., Riedl V., Müllerová J., Kopecký M. & Doležal J. (2013) Tree-rings mirror management legacy: dramatic response of standard oaks to past coppicing in Central Europe. *PLoS ONE* 8(2): e55770.

Dvorský M., Doležal, J. Kopecký M., Chlumská Z., Janatková K., **Altman J**., de Bello F. & Řeháková K. (2013). Testing the stress-gradient hypothesis at the roof of the world: effects of the cushion plant *Thylacospermum caespitosum* on species assemblages. *PLoS ONE* 8: e53514.

Černý T., Song J.-S., Doležal J., Janeček Š., Šrůtek M., Valachovič M., **Altman J**., Petřík P., Bartoš M. & Kolbek J. (2013) Environmental correlates of plant diversity in Korean temperate forests. *Acta Oecologica* 47: 37-45.

Altman J., Doležal J., Černý T. & Song J.S. (2013) Forest response to increasing typhoon activity on the Korean peninsula: evidence from oak tree-rings. *Global Change Biology* 19: 498–504.

Doležal J., **Altman J**., Kopecký M., Černý T., Janeček Š., Petřik P., Bartoš M., Šrůtek M., Lepš J. & Song J-S. (2012) Plant diversity changes during the postglacial in East Asia: insights from forest refugia on Halla Volcano, Jeju Island. *PLoS ONE* 7(3): e33065.

Bartoš M., Janeček Š., Padyšáková E., Patáčová E., **Altman J**., Pešata M., Kantorová J. & Tropek R. (2012) Nectar properties of the sunbird-pollinated plant Impatiens sakeriana: A comparison with six other co-flowering species. *South African Journal of Botany* 78: 63-74.

Janeček Š., Riegert J., Sedláček O., Bartoš M., Hořák D., Reif J., Padyšáková E., Fainová D., Antczak M, Pešata M., Mikeš V., Patáčová E., **Altman J**., Kantorová J., Hrázský Z., Brom J. & Doležal J. (2012) Food selection by floral visitors: an important aspect of plant-flower visitor interactions. *Biological Journal of the Linnean Society* 107: 355-367.

Doležal J., Song J.S., **Altman J**., Janeček Š., Černý T., Šrůtek M. & Kolbek J. (2009) Tree growth and competition in a post-logging Quercus mongolica forest on Mt. Sobaek, South Korea. *Ecological Research*. 24: 281–290.

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