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ORIGINAL PAPER

Fine-scale patch mosaic of developmental stages in Northeast American secondary temperate forests: the European perspective

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Abstract Conceptual models that describe temperate forest dynamics differ substantially between Europe and America. In Europe, the concept of the forest cycle describes a sequentially shifting fine-scale mosaic of patches in different phases of forest development. In North America, the descriptive concept is largely based on severe coarse-scale disturbances that repeat in a cyclic fashion and restart the succession of the whole forest stand from initiation through to 'old-growth,' neglecting the within-stand dynamics on the patch level. Here, we investigate fine-scale stand structures across European and North American forests by applying the European concept of forest developmental phases to all stands. The patches of four major forest developmental stages were recognized and delineated by the spatially explicit rule-based classification system implemented in GIS, which employs stem position maps of live and dead trees for analysis. The basic quantitative characteristics of identified patch structures in the N. American stands, as the Mean Patch Size of the mosaic (between 760 and 890 m^2), were comparable with European old-growth stands, although mosaic complexity was higher in the latter. We demonstrated that in addition to the large-scale forest cycle assumed by N. American conceptual models there simultaneously exist finer-scale patch dynamics described by the European conceptual model. We also demonstrated that the occurrence of the Steady State stage was promoted by higher local tree species richness, which may explain the abundant occurrence of this stage in N. American secondary stands. The Steady State stage of the European model might represent an important commonality across both paradigms.

Keywords Forest cycle · Patch structure · Fine-scale mosaic · Developmental phases · Mean patch size · Successional dynamics

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Introduction

In both Europe and North America, the dynamics of unmanaged temperate forests has been critical to understanding the development and maintenance of these important systems. However, researchers from these two continents employ different conceptual models to describe forest dynamics. The European approach is based on the concept of the forest cycle introduced by Watt (1947), which is characterized by a sequentially shifting fine-scale mosaic of patches in different phases of development within one forest stand. Watt's seminal idea of patch dynamics developed into two recent models of forest dynamics: the patch mosaic model (Leibundgut 1959; Zukrigl et al. 1963; Mayer 1984; Korpel 1995) and the gap-phase model (Runkle 1981; Brokaw 1982; Shugart 1984). Both presume endogenous mortality and/or fine-scale

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disturbances to be the key driving force of forest dynamics. Catastrophic disturbances are considered by these models, though often viewed as deviations from standard stand development.

In North America, the emphasis has been on severe, coarse-scale disturbances (natural or anthropogenic) that initiate even-aged tree populations and their successional pathway (Carey and Curtis 1996; Spies and Franklin 1996; Franklin et al. 2002). These models consider stand-replacing disturbances as an integral part of the structure and function of a temperate forest ecosystem, and that these disturbances are cyclical and restart the succession of the whole forest stand from initiation to a 'climax' (old-growth or steady state) stage (see a review table in Franklin et al. 2002). Some authors suggest that forest stands can persist for long periods in a steady state (Bormann and Likens 1979a) or old-growth stage (Oliver and Larson 1990), where death of one or a few overstory trees acts like a minor disturbance that allows individual recruits or small local cohorts to grow from initial or advanced regeneration to the canopy. Worrall et al. (2005) originated the term bi-cycle dynamics, where the fine-scale cycles are nested within the long-term cycle of severe disturbances. In some regions, the fine-scale cycle can prevail over the large-scale disturbance regime (Frelich and Lorimer 1991). Yet, such fine-scale dynamics have been generally regarded as a single developmental stage (Franklin et al. 2002), usually called shifting-gap phase (Spies and Franklin 1996), steady-state (Bormann and Likens 1979b) or old-growth (Carey and Curtis 1996; Oliver and Larson 1990), without further classification on the patch level (with few exceptions, e.g., Kane et al. 2011).

The divergence of American and European conceptual models may result from evidence that, in some temperate regions of North America, coarse-scale disturbances (especially strong cyclonic winds and forest fires) regularly interrupt autogenic forest development before it reaches the steady state (Bormann and Likens 1979a, b; Oliver and Larson 1990; Linke et al. 2007). Such evidence of coarse-scale disturbances is missing from European temperate forests where low severity winds are the main forest disturbance type (Fischer et al. 2013). The discrepancy between American and European conceptual models may also originate from different approaches to forest management, leading to a lack of continuous forest land under spontaneous development in temperate Europe. Natural coarse-scale disturbances thus may be difficult to detect, because the vast majority of European forests have been subjected to permanent landscape modification (agriculture, urbanization, etc.) and remaining forests have been heavily fragmented by intensive fine-scale silviculture. Consequently, European studies focused on the description of natural forest dynamics in small restricted forest reserves using rather detailed methods such as stem mapping and crown planar projections (e.g., Leibundgut 1982; Průša 1985; Mayer et al. 1989; Korpel 1995). In North America, in contrast, spontaneous succession of forest stands at landscape scale was frequently studied: either after large-scale field abandonment, clear-cuts, forest fires or wind disturbances (e.g., Bormann and Likens 1979b; Oliver and Larson 1990; Frelich 2002), usually using broad-scale methods such as chronosequence and interpretation of aerial photographs. With the development of the ForestGEO Temperate Forest Program initiated in 2007 under the CTFS-ForestGEO global network of forest dynamic plots (Anderson-Teixeira et al. 2014; http://www.forestgeo.si.edu), detailed stem-maps on forested areas larger than 10 ha are available both in Central Europe and temperate North America allowing for fine-scale comparisons.

The principle idea of this paper is thus straightforward but novel. We employed the European conceptual model of the forest cycle to describe fine-scale patch mosaics in North American (hereafter N. American) temperate hardwood secondary forests and compared them with those observed in European deciduous and mixed forests (Král et al. 2014). The use of a uniform approach might contribute to the understanding of commonalities and differences between European and N. American temperate forests. Specifically, we applied the concept of developmental stages and phases (Korpel 1982, 1995), which is commonly followed in central Europe.

Doing so, we are addressing three principle questions:

1. Is it possible to find and describe the fine-scale stand structures in N. American temperate forests by the European conceptual model of the forest cycle?
2. What size, shape and spatial arrangement are the stand structural elements (particular patches) in temperate forest types in North America?
3. Are deciduous and mixed central European forests and N. American temperate deciduous forests comparable in any of the stand structures?

We are aware that there are important differences between the selected European and N. American sites. While the European plots are mostly located in remnants of old-growth forests that have never been intensively cut (Janik et al. 2008, 2013; Vrška et al. 2006, 2012), the N. American plots represent secondary forests developed in less than 130 years of spontaneous succession on abandoned agricultural land (Foster 1992; Foster et al. 1992; Bourg et al. 2013). We therefore hypothesize that the observed patch mosaics will be dominated by fewer stages and formed by larger patches than in European sites. We further hypothesize that the proportion of the Growth stage will be significantly higher, and the proportion of the

Breakdown stage will be significantly lower, than in European sites due to the younger stand ages.

A necessary condition for rigorous comparison of various patch mosaics of forest developmental stages is their objective and fully reproducible distinction and delineation. For that purpose, we originally intended to use the recently developed method based on stem-map artificial neural network (ANN) classifier (Král et al. 2010, 2014). This method, however, works only in IDRISI GIS software and gives comparable results only if an identical training of the ANN is used, which is rather inconvenient for wider applicability and effective sharing. For easier dissemination, we therefore decided to develop and test an alternative rule-based classification providing comparable results and working in widely used ArcGIS. This may be regarded as a specific methodological goal of this study.

Finally, tree species richness is fundamentally different between regions, with European plots having from 6 to 16 species and N. American plots having several times higher species richness. Higher fine-scale tree species richness implies higher fine-scale variability of tree species traits; which likely allows for more possibilities and strategies of neighbor coexistence and thus more variability in stand structures at the finest scales. In 130 years of spontaneous forest succession some old-growth elements might be restored (Oliver and Larson 1990; Vandekerkhove et al. 2009, 2011). We therefore hypothesize that a detectable area of Steady State stage of the European conceptual model will already be developed in the N. American forests, and the higher fine-scale species richness of canopy species will promote the formation of diversified stand structures of Steady State by niche complementarity. More specifically, we asked what the difference is in the occurrence of the Steady State stage at different sites and what the role of tree species richness is in its formation.

Materials and methods

Study sites and datasets

Two N. American temperate secondary forest plots from the CTFS-ForestGEO network (Anderson-Teixeira et al. 2014) were selected to compare with middle European old-growth temperate stands representing alluvial hardwood forests (Ranšpurk and Cahnov plots) and mid-elevation fir-beech forests (Salajka plot). From all sites, we used datasets that include detailed stem mapping (stem coordinates—X, Y), diameter at breast height (DBH), species identification and tree status (dead/alive) of all stems (standing or downed) with DBH ≥10 cm (Table 1).

Smithsonian Environmental Research Center (SERC) plot, USA

The SERC Forest Dynamics Plot is located at the Smithsonian Environmental Research Center in the Mid-Atlantic region (38°53′ N, 76°33′ W) along the western shore of the Chesapeake Bay in Edgewater, Maryland. It lies in the Coastal Plain physiographic province and has a substrate of deep sediments. The site sits close to sea level (0.2–12.0 m elevation range) and is mostly flat (slopes average 8.4 ± 7.2°). However, a stream and its floodplain curve through the plot from the NE to SW. Precipitation, mostly rain, averages 1090 ± 172 mm annually; the mean temperature is 12.8 ± 0.7° C (NOAA regional climatology 1895–2010). The 16.0 hectare (400 m × 400 m) plot established in 2007 is dominated by mature secondary upland forest, but is bisected with a section of floodplain forest. The majority central portion of the plot was most likely a pasture until abandonment in the late 1800s. To the southeast and northwest edges of the central area are younger stands, both of which were fields abandoned in the 1930s. The upland forest is an example of the 'tulip poplar' association with an overstory dominated by tulip poplar (*Liriodendron tulipifera*), several oaks (*Quercus* spp.), beech (*Fagus grandifolia*), and several hickories (*Carya* spp.); a mid-canopy of red maple (*Acer rubrum*) and blackgum (*Nyssa sylvatica*); and an understory composed of American hornbeam (*Carpinus caroliniana*) and paw–paw (*Asimina triloba*). The flood plain forest of the 'river birch-sycamore' group is dominated by ashes (*Fraxinus* spp.), sycamore (*Platanus occidentalis*), spicebush (*Lindera benzoin*) and American elm (*Ulmus americana*). The forest is rather tall (to as high as 40 m) and has a high richness (78 woody species) with 47 species of at least 10.0 cm DBH. Its disturbance history is formed by individual scattered wind-throws and tree falls.

Smithsonian Conservation Biology Institute (SCBI) plot, USA

The SCBI Large Forest Dynamics Plot is located at the Smithsonian Conservation Biology Institute facility in Front Royal, Virginia (38°53′ N, 78°09′ W). The 25.6-ha (400 m × 640 m) plot was established in 2008 and contains 62 species of trees and shrubs. It lies at the intersection of three of the major physiographic provinces of this region: the Blue Ridge, Ridge and Valley, and Piedmont provinces. Before abandonment in early 1900s, the land was considered a pasture, lightly forested on moderate slopes. Dendrochronological data from 492 tree cores suggested the major canopy trees established circa 1900, but scattered trees of several species existed earlier (Bourg

Table 1 Overview of the study plots and used datasets

Site	Location	Elevation range (m)	Mean annual temp. (°C)	Mean annual precip. totals (mm)	Plot size (ha)	Number of living woody stems[a]	Number of woody species[a]	Primary species[b]	Stand age
SERC	USA, Maryland	0–12	13.2	1068	16.0	4668	47	*Fagus grandifolia* *Liriodendron tulipifera* *Liquidambar styraciflua*	ca. 130 years
SCBI	USA, Virginia	273–338	12.9	1001	25.6	8044	48	*Liriodendron tulipifera* *Carya glabra* *Carya tomentosa*	ca. 100–115 years
Cahnov–Soutok	Czech Republic	152–155	9.3	517	17.0	3718	13	*Fraxinus angustifolia* *Acer campestre* *Carpinus betulus*	Old-growth
Ranšpurk	Czech Republic	153–156	9.3	517	22.3	6250	16	*Carpinus betulus* *Acer campestre* *Fraxinus angustifolia*	Old-growth
Salajka	Czech Republic	715–815	5.4	1144	19.0	8782	6	*Fagus sylvatica* *Abies alba* *Picea abies*	Old-growth

[a] Woody stems of DBH ≥ 10 cm

[b] The most frequent woody stems of DBH ≥ 10 cm

et al. 2013). Of the total plot area, 4 ha have had white-tailed deer (*Odocoileus virginianus*) exclusion since 1990. The site is primarily underlain by Myersville and Montalto series silty loam soils, which are stony, steep and well drained. The elevation ranges from 273 m to 338 m a.s.l., and mean annual temperature and precipitation for the area based on a nearby site is 12.7° C and 970 mm, respectively (Bourg et al. 2013). The forest type is a typical mature secondary eastern broadleaf deciduous forest, with a canopy dominated by tulip poplar (*L. tulipifera*), hickories (*Carya* spp.), oaks (*Quercus* spp.) and white ash (*Fraxinus americana*), and an understory composed mainly of spicebush (*Lindera benzoin*), paw–paw (*Asimina triloba*), American hornbeam (*Carpinus caroliniana*) and eastern redbud (*Cercis canadensis*). It is classified as Upper Piedmont/Northern Blue Ridge Basic Mesic Hardwood Forest in the US National Vegetation Classification system (Fleming and Patterson 2012). Its disturbance history is formed by individual scattered wind-throws and tree falls.

European alluvial hardwood forest plots Ranšpurk and Cahnov, Czech Republic

The European alluvial hardwood forests are represented by 22.3-ha plot Ranšpurk (48°40′ N, 16°56′ E) and 17.3-ha plot Cahnov–Soutok (48°39′ N, 16°56′ E; further referred to as Cahnov). Both national nature reserves are located at the confluence of the Morava and Dyje rivers, in the southeastern part of the Czech Republic. The elevation above sea level ranges from 152 to 156 m (Janik et al. 2011). The entire area is an alluvial floodplain, with undulating mounds rising 0.5–3.0 m above the surrounding terrain formed by unwashed down remainders of riverine terraces, which were largely covered by eolian material (sand). The formation of soils was affected by regular inundations that brought flood sediments. Mean annual temperature is 9.3 °C and mean annual precipitation is c. 517 mm. According to the Braun-Blanquet (1921) vegetation classification, plant communities at the sites are

generally classified in the associations *Fraxino pannonicae–Ulmetum* and *Fraxino pannonicae–Carpinetum* (Unar and Šamonil 2008). Stand structure is rich; dominant and codominant canopy trees consist mainly of pedunculate oak (*Quercus robur*) and narrow-leafed ash (*Fraxinus angustifolia*), mid-story and understory is formed by European hornbeam (*Carpinus betulus*), field maple (*Acer campestre*), small-leaved lime (*Tilia cordata*) and others. The forest plots have been left to spontaneous development, avoiding removal of deadwood since the beginning of the 1930s (Vrška et al. 2006). Their disturbance history has been formed mainly by individual tree falls and windthrows, more frequent from 1970 to 1990s due to the simultaneous dieback of the European white elm (*Ulmus laevis*), caused by the Dutch elm disease (*Ophiostoma novo-ulmi*), and in particular by the dieback of an old abundant cohort of pedunculate oak (Janik et al. 2008). The oak dieback was accelerated by the decrease in the water table level due to the elimination of natural spring inundations after 1976 (Penka et al., 1985).

European fir-beech forest Salajka plot, Czech Republic

The 19.0-ha plot of mid-elevation fir-beech forests—Salajka national nature reserve (hereafter Salajka)—lies in the Outer Western Carpathians in the Czech Republic, on the border with Slovakia (49°24′N 18°25′E). The elevation above sea level ranges from 715 to 815 m. The terrain is characterized by slopes of various inclinations (up to 20°) and exposures. Geologically, the entire area belongs to the flysch zone of the Western Carpathians, formed of Godulian Upper Cretaceous sandstones. Prevailing soils are silt loam, loam or occasionally clay-loam Haplic Cambisols (Janik et al. 2014). Mean annual total precipitation is 1144 mm, and mean annual temperature is 5.4 °C (Tolasz et al. 2007). The forests usually belong to the *Dentario enneaphylli–Fagetum* and *Dentario glandulosae–Fagetum* associations (Ellenberg 1996; Šamonil and Vrška 2007). European beech (*Fagus sylvatica*) and to a lesser degree silver fir (*Abies alba*) and Norway spruce (*Picea abies*) dominate the tree species composition. The sites have been strictly protected since the mid-1930s, including no felling or removal of deadwood. The disturbance history has been formed mainly by individual wind-throws and tree falls and from 1970 to 1990s predominately by the dieback of abundant old firs in the Western Carpathians (Vrška et al. 2009) that has been accelerated by air pollution (Tesař and Krečmer 2001).

Data analysis

Rule-based classification of forest developmental stages and phases

In the rule-based classification, we adopted the Korpel's hierarchical concept of developmental stages and phases (Korpel 1982, 1995). Therefore, when henceforth talking about developmental stages and/or phases, we are always referring to this hierarchical concept (Table 2). In case we are referring to the forest developmental phases generally (e.g., citing different authors), it is marked as 'sensu *lato*' in parenthesis.

Like the previous ANN classification (Král et al. 2010, 2014), the rule-based classification developed in this study also employs stem position maps of living and dead trees of DBH ≥10 cm as input data and can therefore be applied on corresponding datasets. Before the classification, basal area (BA) of every tree was calculated by standard formula for calculation of an area of a circle ($BA = \pi\ (DBH/2)^2$). Using GIS focal filtering, the local tree counts and basal areas of both live and dead trees in different DBH classes are calculated separately for every square meter in the stand and its circular surroundings (diameter of the calculation window was 21 m; shifting

Table 2 Grouping of forest developmental stages and phases

Forest developmental phases recognized by the rule-based classification (this study)	Forest developmental phases recognized by the ANN classification (Král et al. 2010, 2014)	Appropriate forest developmental stages (Král et al. 2010, 2014 and this study)
Growth/expiration	Growth/expiration	Growth
Treeless area	Growth initial	
Live tree gap		
Growth initial		
Growth advanced	Growth advanced	
Optimum typical	Optimum typical	Optimum
Optimum aging	Optimum aging	
Breakdown initial	Breakdown initial	Breakdown
Breakdown/regeneration	Breakdown/regeneration	
Steady State	Steady State	Steady State

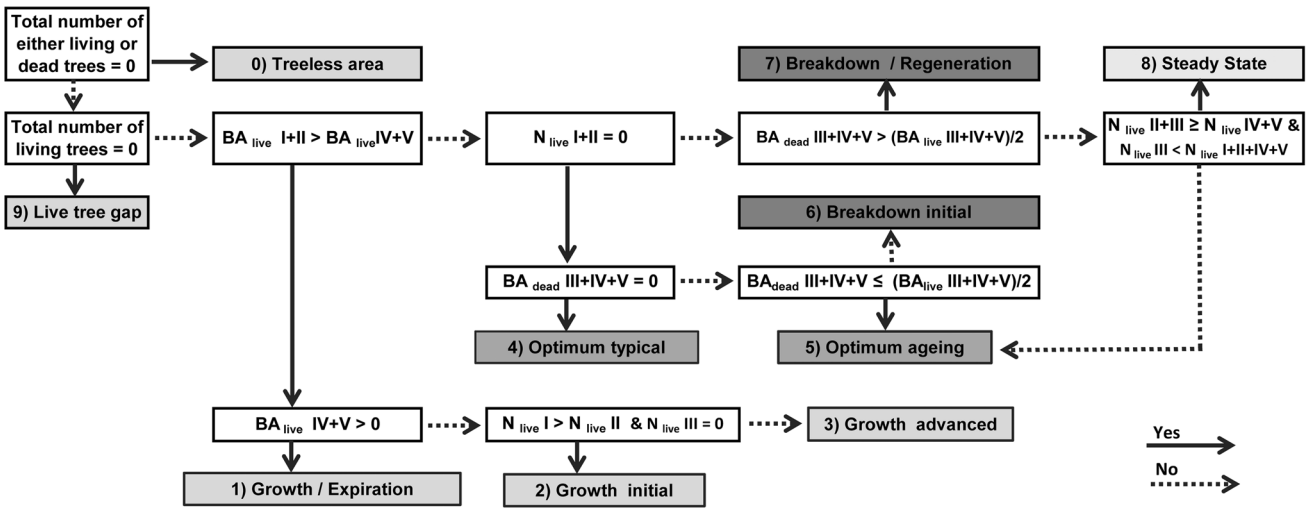


Fig. 1 Simplified flowchart of the rule-based classification of the ten forest developmental phases. Decision rules are in *white boxes* and classification outputs in *grey boxes*. Merging of individual phases into common developmental stages is as follows: 0, 1, 2, 3, 9—Growth stage; 4, 5—Optimum stage; 6, 7—Breakdown stage; 8—Steady State. *N* indicates tree count, *BA* basal area, *roman numerals* in decision rules denote DBH classes (e.g., N_{live} II means number of living trees in DBH class II). *Solid/dashed arrows* signify fulfilled/unfulfilled conditions, respectively

step 1 m). Within the moving window, a local presence/absence and ratios of tree counts and basal areas of live and dead trees in and among different DBH classes are compared. This information is then categorized by the rule-based classification (Fig. 1 and Online Resource 1). An important element in the classification is the definition of DBH classes, which were defined by the predominating canopy class in ascending 5-cm DBH intervals for the N. American plots (see Online Resource 2—Table 1). According to the observations of canopy crown class of each individual from the SERC ForestGEO plot and nearby 4-ha old-growth Frog Canyon plot (Brown and Parker 1994), the DBH classes were defined as follows: 10–20 cm (predominantly suppressed trees); 20–35 cm (predominantly intermediate trees); 35–65 cm (predominantly codominant trees); 65–85 cm (predominantly dominant trees in the ForestGEO plot); and above 85 cm (predominantly dominant trees in Frog Canyon). Significant differences between individual canopy species were not observed there. For European sites, we used the DBH classes defined in Král et al. (2014), i.e., <25, 25–45, 45–65, 65–85 cm and above 85 cm for the beech dominated plot Salajka and robust tree species of the alluvial hardwood plots of Cahnov and Ranšpurk (e.g., pedunculate oak, poplar and narrow-leaved ash). For smaller-statured canopy species (e.g., European hornbeam and field maple), the DBH classes were adjusted according to their total DBH ranges and fitted height curves as follows <20, 20–35, 35–50, 50–65 cm and above 65 cm, taking into account the DBH where the trees usually reach the canopy level (class III). Understory species that never reach the main canopy level were not included in the classification.

The rule-based classification primarily distinguishes ten forest developmental phases that are subsequently regrouped into four major developmental stages (Table 2): Growth, Optimum, Breakdown and Steady State [see also hierarchical nomenclature of Korpel (1995) modified by Král et al. (2010)]. In addition to the eight developmental phases described in Král et al. (2010, 2014), we separated 'Treeless areas' (no trees present) and 'Live tree gaps' (only deadwoods present) as separate phases; both were formerly considered as the starting line of the Initial Growth phase (Table 2). Subsequent analyses of patch mosaics (see below) focused on the four major developmental stages only, which may be defined as follows (Fig. 1 and Fig. 1 of Online Resource 2): The Growth stage is characterized by the local predominance of juvenile and small trees in terms of stem number and also basal area (BA). DBH distribution of living trees is thus characterized by a reverse J-shaped curve. The presence of dead trees (either thin—an indication of stem exclusion; or thick—a mark of previous breakdown) is quite common; however, it is not a determinant feature. The Optimum stage is characterized by the bell-shaped DBH distribution (both for stem number and for BA of trees), though in its aging phase numerous recruits (small understory trees) may occur. In either case, mature and thick trees strongly predominate in the BA of living trees. Similarly, thick dead trees are generally missing. When the local BA of mature dead trees exceeds half of the BA of mature living trees, the area is classified as the Breakdown stage. Lastly, the Steady State is defined by the presence of trees of various sizes where smaller trees are more frequent, but the BA of mature trees dominates. In this stage, the basal area of mature dead trees

is limited to half of the BA of living trees (Fig. 1). Exact complex decision rules defining all forest developmental phases are detailed in the ArcGIS Toolbox (see Online Resource 1).

The accuracy of the rule-based classification and its comparability with the previously used ANN classification was evaluated both on the level of stages and phases by cross-tabulation with reference data in traditional confusion matrices. Producer's and user's accuracy of individual classes and overall accuracy of the classification was calculated (Congalton 1991). As reference data we used: (1) the model samples employed for training of the ANN in the original classification (Král et al. 2014—Appendix A) and (2) the 404 independent evaluation samples representing real stand structures in the Žofín plot (Czech Republic) used by Král et al. (2014). These samples were defined by circular cut outs of the stand position map of Žofín forest; all were examined in the field and their classification thoroughly confronted with quantitative data and empirical knowledge.

Patch mosaics analysis

For easier interpretation and comparability with our preceding studies, we performed the analysis of mosaic patterns only on the level of forest developmental stages. The patch mosaic maps (rasters of pixel resolution of 1 m on the ground) of forest developmental stages resulting from the rule-based classification were generalized by 7 × 7 pixel focal majority filter and analyzed in FRAGSTATS 4.1 (McGarigal and Marks 1995) and in PatchAnalyst 5.0 for ArcGIS software (Rempel et al. 2012) by metrics traditionally used in landscape ecology that are listed below. Patches smaller than 50 m^2 were excluded from the analysis (being empirically regarded as too small to represent a peculiar forest developmental stage). The following mosaic metrics were calculated at class level and mosaic level: Percentage of Stage is the percentage of the total mosaic made up of the corresponding developmental stage, and this index is of necessity calculated only at the class level (%); Mean Patch Size is the average patch size of the class and/or the mosaic (m^2); Largest Patch Index is the percentage of the total class/mosaic area that is made up by its largest patch (%); Mean Shape Index equals 1 when all patches of the corresponding patch type are circular and increases without limit as the patch shapes become more irregular; Interspersion and Juxtaposition Index measures the observed interspersion compared with the maximum possible interspersion for the given number of patch types (%) and is based on edge adjacency of different patch types (it equals 100 when all patch types are equally adjacent to all other patch types); Shannon's Evenness Index measures the evenness of the area distribution among different patch types, and it approaches 0 when the mosaic is dominated by one patch type and increases up to 1 as the distribution of area among different patch types is increasingly even (this index is of necessity only available at the mosaic level). Precise definitions including formulas of used mosaic metrics are given by McGarigal and Marks (1995).

For assessing simplicity/complexity of observed patch spatial patterns, we adopted the concept of Wiens (1995) further elaborated by Kane et al. (2011) which distinguishes among homogenous structure, matrix–patch structure and patch mosaic structure (i.e., from the dominance of a single or few large patches to a fine-scale mosaic mixed of many patch types). For that we used Shannon's Evenness Index as a measure of (un)even areal participation of individual patch types, Interspersion and Juxtaposition Index as a measure of spatial interspersion of different patch types and Largest Patch Index as a measure of the dominance of large patches within each plot.

The differences among mosaic metrics were compared with bootstrap confidence intervals, which provide very effective nonparametric analyses of uncertainty and sensitivity and allow inference about the robustness of the results. The 95 % nonparametric bias-corrected and accelerated (BCa) confidence intervals based on 999 bootstrap replications, i.e., the interval estimates of the variable means at the significance level $\alpha = 0.05$, were constructed for mean values of Mean Patch Size and Mean Shape Index and for percentages of Largest Patch Index and Percentage of Stage. The BCa limits were given by percentiles of the bootstrap distribution. The percentiles used depend on acceleration and bias correction (Efron and Tibshirani 1993; Miller 1964). When the confidence intervals overlapped, the results were not considered statistically different. In this manner, we also verified whether the original ANN classification (Král et al. 2014) and the new rule-based classification produced patch mosaics of comparable metrics. The 'bootstrap' package of R statistical software (Efron and Tibshirani 1993; R Development Core Team 2015) was used for these calculations.

Effect of tree species richness on Steady State formation

The relation between the tree species richness and the Steady State stage was evaluated through a generalized linear model in R statistical software (R Development Core Team 2015). The logistic regression model regressed the status of a cell (Steady State stage [1] or Not [0]) against standardized (x.new = (x − mean(x))/sd(x)) measures of species richness and stem density. An interaction term (in addition to the main effects) incorporated the covariance between species richness and stem density. This was a generalized linear model with binomial error distribution and logit link conducted at each site separately. As the

response variable for the GLM was Bernoulli in distribution, there was no overdispersion to test for. Although the sites differed in area (Table 1), all contained enough power to resolve this relationship (Table 3). Because the species richness, stem density and their effect on forest functions are scale specific (Chisholm et al. 2013), it was measured exactly at the same scale as was used for classification of developmental stages, i.e., 21-m circular moving window was used for local tree species richness and stem density calculations. Spatial autocorrelation was removed by selecting a subset of points across the plots that maintained a 20 m distance. In all plots, semivariograms of spatial autocorrelation showed that this sampling distance removed all spatial correlation in the variables of interest (species richness, stem density).

Results

Accuracy and generalization of the rule-based classification

The rule-based classification categorized more than 95 % of the 540 typical samples of the eight developmental phases used for learning the ANN in Král et al. (2014) into the concordant developmental phase. When distinguishing only four major developmental stages, almost 98 % of the samples were classified accordingly; producer's accuracies of individual developmental stages were always above 90 %. When we evaluated the performance of the rule-based classification by 404 samples representing real stand structures in the Žofín forest (Král et al. 2014), the calculated overall accuracies were somewhat lower: reaching 81 % for eight developmental phases and 88 % for four developmental stages. For further details, see the DBH distributions of mapped forest developmental stages and complete confusion matrices (Fig. 2; Tables 2–5 in Online Resource 2).

No less important than the overall accuracy of the rule-based classification approach is the comparability of derived mosaic metrics with those of the original ANN classification. Although there are some differences between results of the two methods, they are, with few exceptions, insignificant (see Fig. 3 in Online Resource 2). The proportions of individual stages in the mosaics are not remarkably different (confidence intervals do overlap). Also, the Mean Patch Size and Mean Shape Index of the total mosaic are consistent. Slight systematic (but usually insignificant) shifts are apparent in the decrease in Percentage of Stage, Mean Patch Size, Largest Patch Index and Mean Shape Index of the Steady State stage in the rule-based classification. This is not a problem as the Steady State used to be slightly overestimated by the original ANN classification.

Fig. 2 Patch mosaic metrics for the four forest developmental stages ▶ and mosaic as a whole in the two plots of the N. American east coast (SERC, SCBI) compared to the three central European plots (Cahnov—CA, Ranšpurk—RN, Salajka—SL); metrics: Percentage of Stage in the stand (**a**), Mean Patch Size (**b**), Largest Patch Index (**c**) and Mean Shape Index (**d**). *Black squares* represent the mean values, and *whiskers* represent its 95 % bootstrap BCa confidence intervals. When the confidence intervals overlap, the results are not considered significantly different

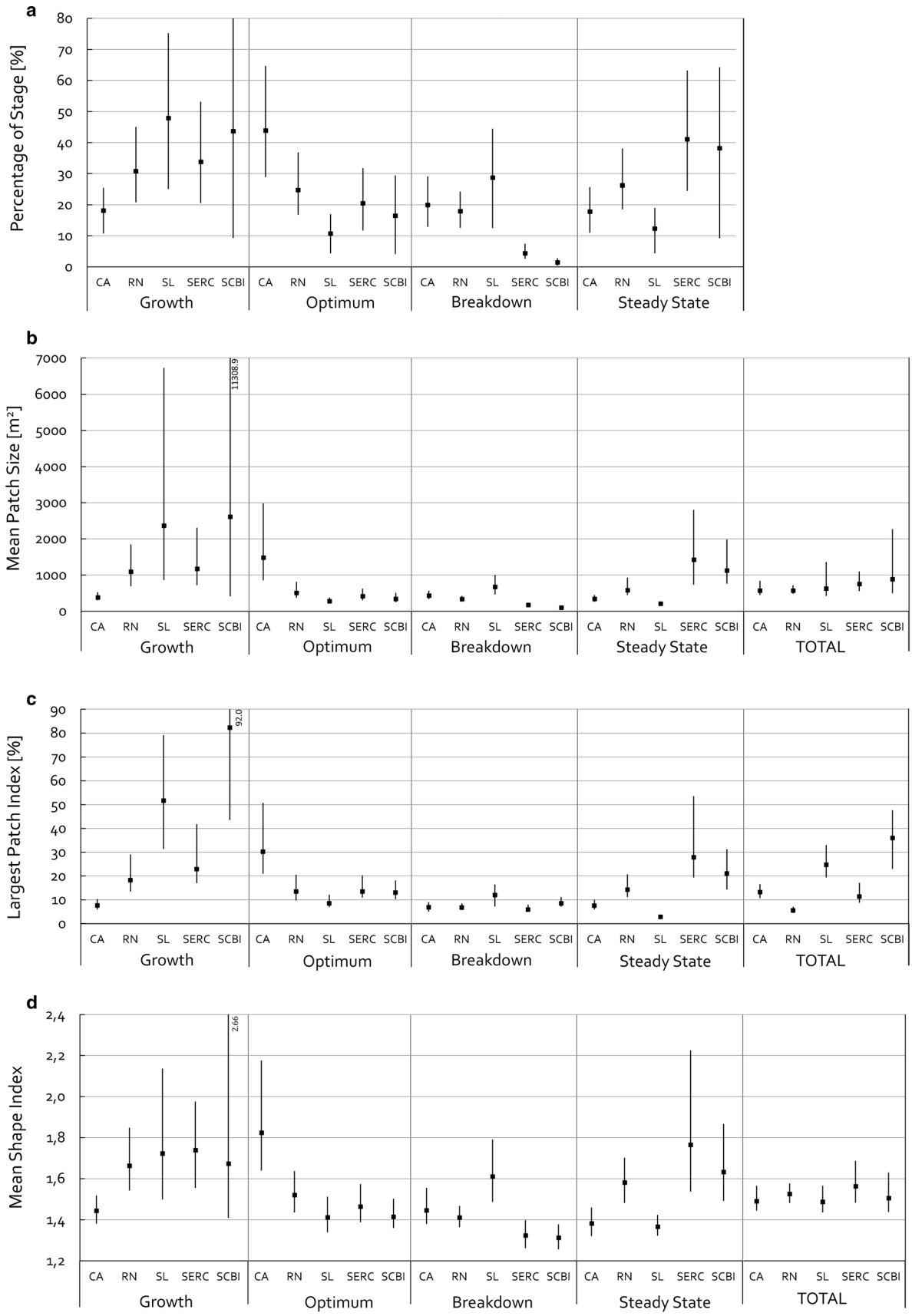
Patch mosaic in N. American east coast secondary temperate forests

The stand mosaic in both N. American plots is predominantly formed by the Growth and the Steady State stages, which together cover 75 % of SERC plot and 82 % of SCBI plot (see Figs. 2, 3). The Growth stage forms 34 and 44 % of the stand mosaic at SERC and SCBI, respectively, and the Steady State stage covers 41 and 38 % of these stands. The Optimum stage forms a smaller part of the stands—about 21 % in SERC and 17 % in SCBI. The Breakdown stage covers markedly the smallest areas of the stands—its proportion ranges from 1.5 to 4.5 %. Similar patterns may be observed in Mean Patch Sizes (herein together with ± standard error of the mean), which are largest for the Growth stage (about 1180 ± 329 m^2 in SERC and 2618 ± 2124 m^2 in SCBI) and the Steady State (about 1430 ± 477 m^2 in SERC and 1130 ± 286 m^2 in SCBI). Mean Patch Sizes of other stages are much smaller: for the Optimum stage about 420 ± 76 m^2 in SERC and 340 ± 62 m^2 in SCBI, and for Breakdown stage only

Table 3 Results from the logistic regression of the presence of Steady State (0/1) using a binomial link function. The explanatory variables of tree species richness, stem density and their interaction, all standardized to unit scale

Site	Intercept	Sp. richness	Stem density	Sp. richness: Stem density	Degrees of freedom
Cahnov	−1.72***	0.60**	0.93***	−0.52***	439
Ranšpurk	−1.26***	1.01***	0.10	−0.20	566
Salajka	−1.89***	0.61***	−0.39*	−0.12	470
SERC	−0.38**	0.50***	0.34*	−0.36**	399
SCBI	−0.37***	0.13	0.47***	−0.37***	639

Significance codes: *** p value < 0.001; ** p value < 0.01; * p value < 0.05; values without asterisk had p values > 0.1



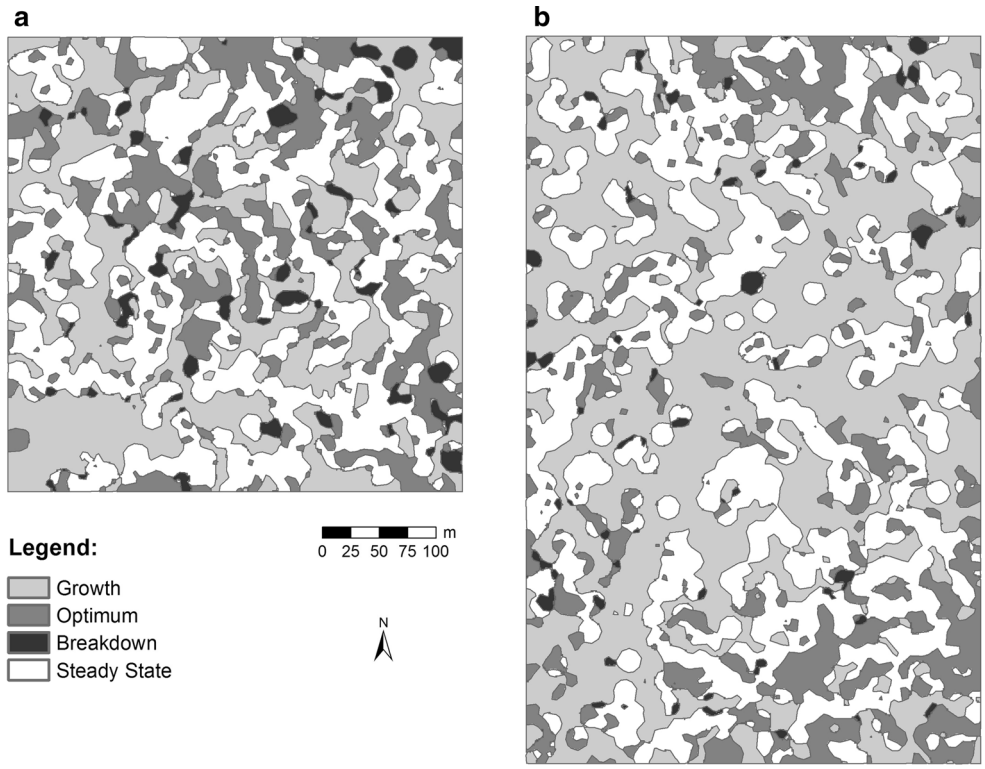


Fig. 3 Mosaic of forest developmental stages in SERC (**a**) and SCBI (**b**) ForestGEO plots representing N. American secondary temperate forests of the east coast

between 100 ± 12 and 180 ± 16 m^2 in both plots. Mean Patch Size of the total mosaic is about 760 ± 134 m^2 in SERC and 890 ± 331 m^2 in SCBI.

The Largest Patch Index shows a similar pattern, usually varying between 20 and 30 % for both the Growth stage and the Steady State. In SCBI, the Largest Patch Index of the Growth stage reaches an exceptional 82 %; indicating that a large extent of this area is formed by a single patch (Fig. 3b). Since Growth is the abundant stage, it leads to a high Largest Patch Index value of the whole mosaic in the SCBI plot (36 %). At SERC, the Largest Patch Index of the mosaic is ca 12 %. Largest Patch Index of the Optimum stage is between 13 and 14 % and ranges between 6 and 9 % for the Breakdown stage in both plots.

The Mean Shape Index, which is increasing with shape complexity of patches from 1.0 for purely circular shape, is again markedly larger for the Growth stage and the Steady State (mean values ± standard error of the mean are between 1.63 ± 0.09 and 1.77 ± 0.16 in both plots); in contrast, it is the smallest for the Breakdown stage with the value of 1.31 ± 0.03. Mean Shape Index of the Optimum stage is about 1.43 ± 0.04 and of the total mosaic about 1.53 ± 0.05.

Comparison with European temperate forests

For the total mosaic (i.e., evaluating all patches irrespective of the stage), the Mean Patch Sizes in N. American plots (especially SCBI) are slightly higher than in the European plots, though the differences are within overlapping confidence intervals (Fig. 2). The Mean Shape Index of patches is quite comparable in N. American and European sites. A difference lies in the Largest Patch Index, which is remarkably higher at SCBI due to the extensive matrix of the Growth stage (Fig. 3b), indicating higher simplicity of the patch mosaics at N. American secondary stands (matrix–patch structure in sense of Wiens 1995). This phenomenon is demonstrated also by Shannon's Evenness Index and the Interspersion and Juxtaposition Index—their lower values are indicative of increased disproportionality among areas of different patch types and their lower spatial interspersion, respectively (Fig. 4).

On the level of individual developmental stages, there are some differences between N. American secondary growth and European old-growth stands. There is a considerably smaller proportion of the Breakdown stage in both N. American plots (1-5 %) compared to levels observed in Europe (about 20 %). Moreover, the patches of the Breakdown stage are significantly smaller (Fig. 2). In contrast, the proportion of the Steady State is somewhat surprisingly high (41 % for SERC and 38 % for SCBI) and formed by the patches that are mostly larger (see Mean Patch Size and Largest Patch Index) and often of more complex shape (Mean Shape Index) than in European sites. Yet, we should keep in mind that these metrics are inevitably correlated—higher abundance of any class is likely to

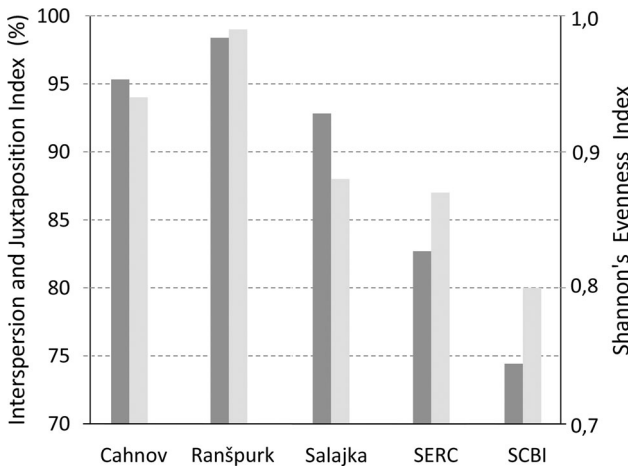


Fig. 4 Comparison of mosaic simplicity/complexity by means of the Interspersion and Juxtaposition Index (*dark grey*) and Shannon's Evenness Index (*light grey*)

produce bigger patches, which further tend to have more complex shape. More abundant classes are also likely to have higher connectivity. The patches of the Optimum stage are smaller and of simpler shape than in European sites, though not always significantly. The metrics of the Growth stage are usually comparable with European old-growth stands.

The link between Steady State and species richness across sites

The regression output showed that across sites, observed associations between the local species richness of canopy trees, stem density and the probability of a location being classified as Steady State differed across sites, but with some common patterns (Fig. 5; Table 3). In all plots except SCBI, local tree species richness was a highly significant positive predictor of Steady State occurrence (Table 3). Local stem density was a significant positive predictor of Steady State occurrence only in Cahnov, SERC and SCBI. However, at those plots the species richness and stem density had a negative interaction effect, indicating that increases in either variable would weaken the relationship with Steady State occurrence for the other. The predictive plots of the response variable for those sites thus appear as 'twisted' between diagonal corners of the predictive space (Fig. 5a, d, e). The strong positive correlation between species richness and the Steady State was manifested at

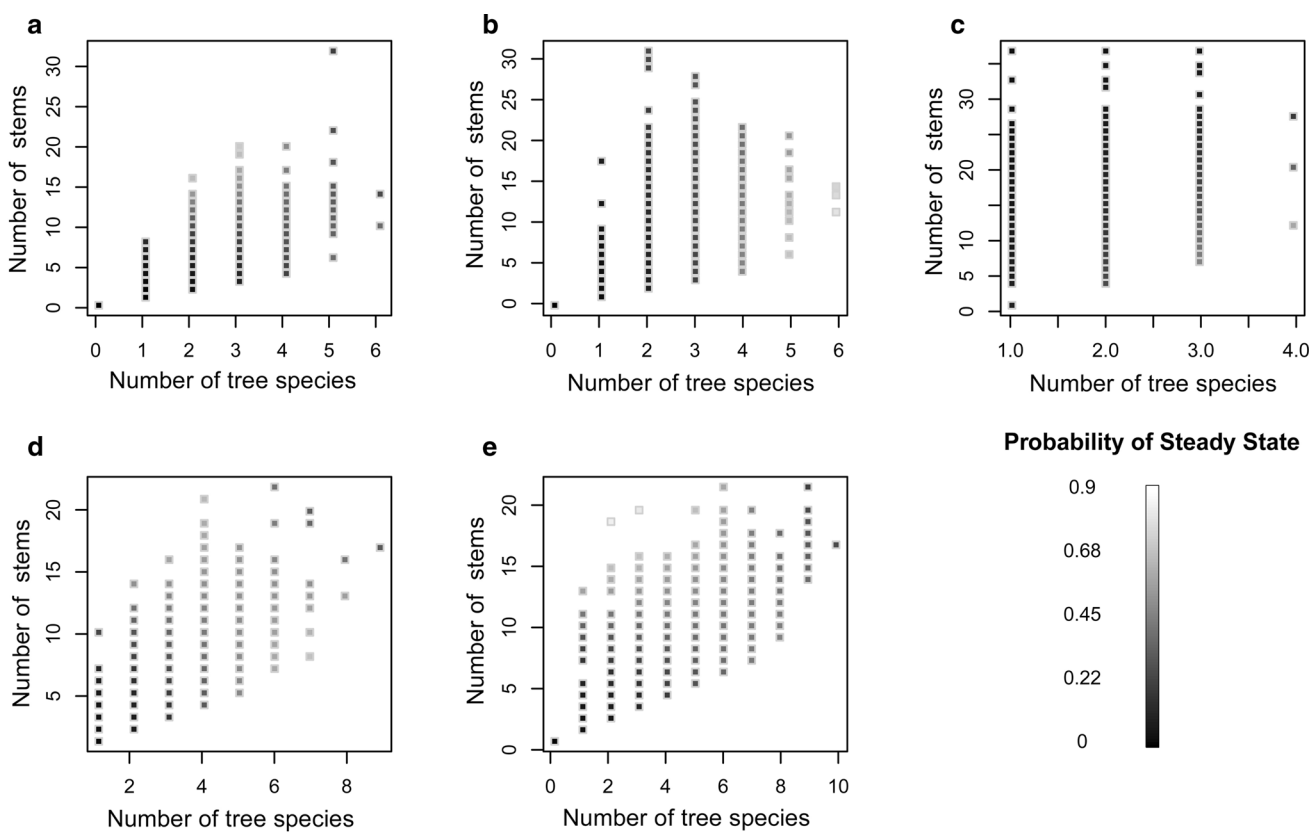


Fig. 5 Predictive plot of the response interaction between local species richness and stem density on the probability of Steady State occurrence across the five study plots: Cahnov (**a**), Ranšpurk (**b**), Salajka (**c**), SERC (**d**) and SCBI (**e**). Number of tree species and number of stems refer to the area of the moving window (circle of 21 m in diameter)

low stem densities and vice versa. Furthermore, the significant positive correlation between stem density and the Steady State was registered at low species richness and vice versa.

At Ranšpurk and Salajka plots, the increase in the probability of Steady State with species richness was independent of a basic increase in stem density (interaction effect was insignificant; see Table 3). The predictive plots of the response variable were simpler, (Fig. 5b, c) showing that tree species richness had the strongest association with Steady State.

The total species richness of N. American and European plots was very different (Table 1). The local species richness within the moving filter was much closer, though still significantly higher at N. American plots than at European plots. The mean values of local species richness (±standard error of the mean) were as follows: 3.96 ± 0.08 at SERC; 4.85 ± 0.08 at SCBI; 1.86 ± 0.04 at Salajka, 2.60 ± 0.07 at Cahnov and 2.80 ± 0.05 at Ranšpurk. This also might be associated with the overall occurrence of Steady State across the plots (Fig. 2) and the different relationships between stem density and species richness.

Discussion

Effective spatially explicit rule-based classification of forest developmental stages and phases

The rule-based classification of forest developmental phases (sensu lato) is a common approach used in European temperate forests (e.g., Winter and Brambach 2011). In this paper, we introduced the new spatially explicit rule-based classification based on the moving window technique. It means that the rules demonstrated in Fig. 1 are applied independently on every square meter of the stand and its circular surroundings. The mapping procedure is highly automated and works without any pre-defined grid, as is common in other studies—e.g., grid of 12.5 m × 12.5 m used by Tabaku (2000) or 11.18 m × 11.18 m used by Winter and Brambach (2011). Accordingly, neither the smallest identifiable unit nor the patch borders are predefined as in grid-based methods and may better follow stand structures present in the forest. At the same time, our method is purely quantitative, avoiding questionable classification based on field estimates (e.g., Begehold et al. 2016; Bobiec et al. 2000), and thus ensures complete repeatability and comparability of mapping. The employed rules are always based on the presence/absence and ratios (proportions) of tree counts and basal areas of live and dead trees in and among various DBH classes. Absence of specific tree numbers and basal areas facilitates the transferability of the rules in forest types with different tree densities and maximal tree sizes. In such a case, an adjustment of DBH classes to specific forest conditions is recommended. Fixed DBH classes irrespective of forest type, regional conditions and significantly different species traits might cause substantial biases (cf. redwoods of the west coast and Mediterranean forest). The parameter of tree species is not directly included in the classification algorithm, but the algorithm allows the use of alternative DBH classes for different species groups if needed (such a setup was used in Cahnov and Ranšpurk plots). We intended a wider applicability of the new method introduced here; therefore, it was implemented in the ArcGIS 10 Toolbox and the user defined toolbox called 'Phase Classifier' is available as Online Resource 1. This complex and adjustable GIS tool can transform any stem position map, which includes not only living trees, but also standing and lying deadwood, into the maps of developmental stages and phases and may be considered as a by-product of this paper. Results are then presented as raster maps (1 m pixel TIFFs) of ten forest developmental phases and 4 forest developmental stages in a raw form and in a form smoothed by 7 × 7 pixel majority filter reducing a 'salt and pepper' effect of the raw classification. The general problems in mapping of forest developmental phases (sensu *lato*) are differences in systems and/or loose definitions of categories used by different authors (Standovár and Kenderes 2003). Sharing of a common published tool among research groups across Europe might lead to desired harmonization and standardization.

In N. American hardwood forests, Lorimer and Halpin (2014) also used the rule-based approach for classification of developmental stages (sensu *lato*). Their approach, however, was not spatially explicit—each of their 0.5-ha study plots was classified in one stand developmental stage. Their classification was thus performed at the stand scale not addressing the fine-scale patch pattern within the stand. Lorimer and Halpin (2014) also assumed that their classification is not generally applicable in forests in which fast growing species such as *L. tulipifera* are mixed with slow-growing species of high shade tolerance. Our analyses, however, did not reveal any significant difference between light-demanding and shade-tolerant canopy tree species either in fitted height curves (DBH vs. height relation) or in prevailing canopy status (see Fig. 4; Table 1 of Online Resource 2). We thus believe that common rules for all canopy species were in this case applicable.

Commonality and variability of observed stand structures

The mosaics of the two N. American secondary temperate forests were in most characteristics comparable with those observed in central European old-growth forests. The

major difference was a significantly lower occurrence of the Breakdown stage in N. American stands. This was expected as N. American stands have less than 130 years since stand initiation and are therefore still predominantly in a building phase. Substantial degrading processes are still about to come as the period of secondary succession will be approaching the life span of canopy tree species. The observed Mean Patch Sizes of the Breakdown stage (100–180 m^2) were comparable to the mean gap sizes reported from N. American temperate hardwood forests (McCarthy 2001). These patches of the Breakdown stage are thus likely formed by single fine-scale disturbances (canopy gaps), as opposed to the Breakdown patches in European old-growth stands that are noticeably larger (300–700 m^2) and are most likely formed by clumping of several canopy gaps (Král et al. 2014).

Further, although the N. American stands are much younger, all major developmental stages have already developed, and so the number of different patch types forming the mosaic of forest developmental stages in European and N. American stands was the same. Higher simplicity of N. American patch mosaics is thus given by the predominance of one or two stages, which is reflected in the Shannon's Evenness Index and by lower spatial interspersion of different stages that is reflected in the Interspersion and Juxtaposition Index (Fig. 4). To get a visual sense of how different the mosaics are in addition to the differences indicated by the indices, see Fig. 3 and compare with Fig. 5 of Online Resource 2 (e.g., interconnected matrix of the Growth stage with very rare inclusions of Breakdown in N. American plots vs. more even representation of all developmental stages in the European plot). Establishment of the complex mosaic pattern thus may take much longer than the establishment of individual patches of all major developmental stages, including the Steady State stage (see below). Similar conclusions were made by Kane et al. (2011) who found the larger-scale variability, i.e., the patch mosaic structure sensu of Wiens (1995) appeared to be a pattern unique to old-growth forests that was missing in the secondary stands. The uniqueness of high larger-scale variability of canopy structures to old growth stands was reported already by Cohen et al. (1990) from aerial photographs. The effect of stand age (i.e., length of the secondary succession) on the observed patch patterns was also indicated on the SCBI plot—as the youngest plot it seems to have the simplest patch mosaic with high proportion of the Growth stage, the smallest proportion of the Breakdown stage and the highest Largest Patch Index (the background matrix of Growth stage was the most apparent). Also the spatial interspersion of different stages and evenness of the area distribution among different patch types are the lowest at SCBI. The differences found between European and N. American mosaics are thus, besides the different tree species richness (see below), primarily caused by different ages of European and N. American plots.

Against our prediction, we found that the proportion of the complete forest found in the Growth stage was not markedly higher in the N. American stands than in the European old-growth stands. On the other hand, the proportion of the Steady State stage, which characterizes locally the most complex stand structures, was comparable with (or higher than) observations in European natural forests with high continuity of development. The patches forming the Steady State in N. American secondary forests were generally larger than in European old-growth stands, even though the forests are 'younger' overall. This pattern might relate not to stand age, or stem density, but the tree species richness at a site. This would follow from the functional redundancy of many species through niche complementarity over successional development (Fargione et al. 2007). Even a young forest, therefore, would be more likely to exhibit many successional stages in a small area not because of long-term dynamics per se, but due to the different ages of the cohorts of species in the course of secondary succession at N. American sites. The greater the species number, the more likely that local cohorts are unsynchronized and therefore contribute to a more varied total community tree size distribution. The higher total and local tree species richness of N. American stands is thus the likely explanation of relatively abundant occurrence of the Steady State stage there.

This was generally supported in our analysis. Within all sites, except for the youngest (SCBI), species richness was positively associated with steady state. Even at SCBI, the trend was positive, but when we took into account the sampling effect of stem number (the higher the stem density, the higher the likelihood of multiple species) then the effect of species richness disappeared. The interaction effect thus helps disentangle the fact that with more stems, one might expect (and does see) higher species richness. With the interaction term, we take out that effect and still see the relationship between richness and steady state. For all other sites, species richness maintained a strong positive effect on Steady State occurrence. These findings are in line with the results of Pretzsch and Schütze (2016), who found higher right skewness and kurtosis of the tree size distribution, higher inequality of tree sizes and thereby higher stocking densities (i.e., the properties typical for Steady State stage) in mixed species compared to monospecific stands, all explained by the complementary species-specific ecological traits in mixed stands. The effect of neighborhood niche complementarity on stand structure and growth was recently documented in temperate (e.g., Morin et al. 2011) as well as in tropical forests (e.g., Chisholm et al. 2013; Chen et al. 2016).

However, there are at least two pathways of Steady State formation (see Fig. 5). The first pathway occurs when the stem density is low and is based on the local species richness and refers to the niche complementarity. A low local stem density indicates a relatively closed canopy, and in such a case a wide range of tree sizes typical for the Steady State stage (i.e., local presence of trees of various DBH classes at a time) might be better maintained by high species richness, because a combination of species with complementary ecological traits enables a coexistence of trees of variable sizes in different canopy layers (Pretzsch and Schütze 2016). The second pathway was identified only at some plots (see Fig. 5a, d, e) and applies at higher local stem density, which may be a result of past fine-scale canopy disturbance. The disturbance had to be small enough to preserve some mature trees, but big enough to simultaneously allow recruitment of relatively abundant juvenile and understory trees at the same place. In these cases, usually only a few species benefited from the local disturbance by release and regeneration, and thus, these cases are negatively correlated with local species richness. Under this scenario, the Steady State formation supports the intermediate disturbance hypothesis (Connell 1978). The relationship between species richness, intermediate disturbance regime and patch type of the forest cycle was found in a tropical montane rain forest by Zang et al. (2005); however, they did not distinguish Steady State as one of the patch types.

Conclusions

This paper demonstrates that N. American temperate forests can be understood and quantified as a fine-scale mosaic of developmental dynamics. The fine-scale patch patterns of forest developmental stages were identified in two large plots, which are representative of secondary temperate deciduous forests of the US east coast. In less than 130 years of secondary succession, all major 'European' forest developmental stages have already developed and formed the patch mosaic there. Because complexity of these mosaics seems to increase with the stand age, the observed patch mosaic will most likely proceed and develop through the succession until the old growth. We thus demonstrated that besides the large-scale forest cycle accented by N. American conceptual models there simultaneously exists a finer-scale patch dynamics describable by the European conceptual model. This is a novel contribution of the European concept of forest dynamics to the N. American concept, where entire stands are usually considered to be in one developmental stage. Our results indicated that the mosaic complexity increases along the age of forest stands. It would be interesting to analyze and compare also fine-scale patch mosaics of N. American old-growth stands (both of east and west coast). We also believe that presented description of patch structures might be interesting for more general applications.

Our preceding study (Král et al. 2014) showed the importance of the Steady State stage, characterized by locally rich and diversified stand structure that likely plays a more important role in overall dynamics of European temperate forests than previously thought. Our recent results indicate this stage may be even more important for N. American temperate forests. This 'all in one stage' of the European model might represent an important commonality across European and N. American concepts of forest dynamics as a fine-scale analogy to the N. American 'old-growth' stage. Although at different spatial scales, they both reflect, in effect, a de facto mosaic of stages.

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References

Anderson-Teixeira KJ, Davies SJ, Bennett AC et al (2014) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. Global Change Biol 21:528–549. doi:10.1111/gcb.12712

Begehold H, Rzanny M, Winter S (2016) Patch patterns of lowland beech forests in a gradient of management intensity. For Ecol Manag 360:69–79

Bobiec A, van der Burgt H, Meijer K, Zuyderduyn C, Haga J, Vlaanderen B (2000) Rich deciduous forests in Bialowieza as a dynamic mosaic of developmental phases: premises for nature conservation and restoration management. For Ecol Manag 130:159–175

Bormann FH, Likens GE (1979a) Catastrophic disturbance and the steady state in northern hardwood forests. Am Sci 67:660–669

Bormann FH, Likens GE (1979b) Pattern and process in a forested ecosystem. Springer, New York

Bourg NA, McShea WJ, Thompson JR, McGarvey JC, Shen X (2013) Initial census, woody seedling, seed rain, and stand structure data for the SCBI SIGEO Large forest dynamics plot. Ecology 94:2111

Braun-Blanquet J (1921) Prinzipien einer Systematik der Pflanzengesellschaften auf floristischer Grundlage. Jahrbuch der St. Gallischen Naturwissenschaftlichen Gesellschaft 57:305–351

Brokaw NV (1982) The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 14:158–160

Brown MJ, Parker GG (1994) Canopy light transmittance in a chronosequence of mixed-species deciduous forests. Can J For Res 24:1694–1703

Carey AB, Curtis RO (1996) Conservation of biodiversity: a useful paradigm for forest ecosystem management. Wildl Soc B 24:610–620

Chen Y, Wright SJ, Muller-Landau HC, Hubbell SP, Wang Y, Yu S (2016) Positive effects of neighborhood complementarity on tree growth in a Neotropical forest. Ecology 97:776–785

Chisholm RA, Muller-Landau HC, Abdul Rahman K et al (2013) Scale-dependent relationships between tree species richness and ecosystem function in forests. J Ecol 101:1214–1224

Cohen WB, Spies TA, Bradshaw GA (1990) Semivariograms of digital imagery for analysis of conifer canopy structure. Remote Sens Environ 34:167–178

Congalton RG (1991) A review of assessing the accuracy of classifications of remotely sensed data. Remote Sens Environ 37:35–46

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Development Core Team R (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Efron B, Tibshirani R (1993) an introduction to the bootstrap. Chapman & Hall/CRC, Boca Raton

Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Eugen Ulmer, Stuttgart

Fargione J, Tilman D, Dybzinski R et al (2007) From selection to complementarity: shifts in the causes of biodiversity–productivity relationships in a long-term biodiversity experiment. Pro R Soc Lond B Biol Sci 274:871–876

Fischer A, Marshall P, Camp A (2013) Disturbances in deciduous temperate forest ecosystems of the northern hemisphere: their effects on both recent and future forest development. Biodivers Conserv 22:1863–1893

Fleming GP, Patterson KD (2012) Natural communities of Virginia: ecological groups and community types. Natural Heritage Technical Report 12–04. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, Virginia, USA

Foster DR (1992) Land-use history (1730–1990) and vegetation dynamics in central New England, USA. J Ecol 80:753–772

Foster DR, Zebryk T, Schoonmaker P, Lezberg A (1992) Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. J Ecol 80:773–786

Franklin JF, Spies TA, Pelt RV et al (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For Ecol Manag 155:399–423

Frelich LE (2002) Forest dynamics and disturbance regimes. Cambridge University Press, Cambridge

Frelich LE, Lorimer CG (1991) A simulation of landscape-level stand dynamics in the northern hardwood region. J Ecol 79:223–233

Janik D, Adam D, Vrska T, Hort L, Unar P, Kral K et al (2008) Tree layer dynamics of the Cahnov–Soutok near-natural floodplain forest after 33 years (1973–2006). Eur J For Res 127:337–345

Janik D, Adam D, Vrska T, Hort L, Unar P, Kral K, Samonil P, Horal D (2011) Field maple and hornbeam populations along a 4-m elevation gradient in an alluvial forest. Eur J For Res 130:197–208

Janik D, Adam D, Hort L, Kral K, Samonil P, Unar P, Vrska T, Horal D (2013) Spatiotemporal differences in tree spatial patterns between alluvial hardwood and mountain fir-beech forests: do characteristic patterns exist? J Veg Sci 24:1141–1153

Janik D, Adam D, Hort L, Kral K, Samonil P, Unar P, Vrska T (2014) Tree spatial patterns of *Abies alba* and *Fagus sylvatica* in the Western Carpathians over 30 years. Eur J For Res 133:1015–1028

Kane VR, Gersonde RF, Lutz JA, McGaughey RJ, Bakker JD, Franklin JF (2011) Patch dynamics and the development of structural and spatial heterogeneity in Pacific Northwest forests. Can J For Res 41:2276–2291

Korpel S (1982) Degree of equilibrium and dynamical changes of the forest on example of natural forests of Slovakia. Acta Fac For 24:9–30

Korpel S (1995) Die Urwälder der Westkarpaten. Gustav Fischer Verlag, Stuttgart

Král K, Vrška T, Hort L, Adam D, Šamonil P (2010) Developmental phases in a temperate natural spruce-fir-beech forest: determination by a supervised classification method. Eur J For Res 129:339–351

Král K, McMahon SM, Janík D, Adam D, Vrška T (2014) Patch mosaic of developmental stages in central European natural forests along an elevation and vegetation gradient. For Ecol Manag 330:17–28

Leibundgut H (1959) Über Zweck und Methodik der Struktur und Zuwachsanalyse von Urwäldern. Schweizerische Zeitsschrift für Forstwesen 110:111–124

Leibundgut H (1982) Europäische Urwälder der Bergstufe. Haupt, Bern

Linke J, Betts G, Lavigne B, Franklin SE (2007) Introduction: structure, function, and change of forest landscapes. In: Wulder A, Franklin SE (eds) Understanding forest disturbance and spatial pattern. Taylor & Francis, Abingdon, pp 1–29

Lorimer CG, Halpin CR (2014) Classification and dynamics of developmental stages in late-successional temperate forests. For Ecol Manag 334:344–357

Mayer H (1984) Wälder Europas. Gustav Fischer Verlag, Stuttgart

Mayer H, Zukrigl K, Schrempf W, Schlager G (1989) Urwaldreste, Naturwaldreservate und schützenswerte Naturwälder in Österreich. Universität für Bodenkultur, Wien

McCarthy J (2001) Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ Rev 9:1–59

McGarigal K, Marks BJ (1995) FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. General Technical Report PNW-GTR-351, USDA Forest Service, Pacific Northwest Research Station, Portland

Miller RG (1964) A trustworthy jackknife. Ann Math Stat 35:1594–1605

Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol Lett 14:1211–1219

Oliver CD, Larson BC (1990) Forest stand dynamics. McGraw-Hill Inc, New York

Penka M, Vyskot M, Klimo E, Vašíček F (1985) Floodplain forest ecosystems I: before water management measures. Academia, Prague

Pretzsch H, Schütze G (2016) Effect of tree species mixing on the size structure, density, and yield of forest stands. Eur J For Res 135:1–22

Průša E (1985) Die bömischen und mährischen Urwälder—ihre Struktur und Ökologie. Academia, Praha

Rempel RS, Kaukinen D, Carr AP (2012) Patch analyst and patch grid. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario

Runkle JR (1981) Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041–1051

Šamonil P, Vrška T (2007) Trends and cyclical changes in natural fir–beech forests at the North-western Edge of the Carpathians. Folia Geobot 42:337–361

Shugart HH (1984) A theory of forest dynamics. Springer, New York

Spies TA, Franklin JF (1996) The diversity and maintenance of old-growth forests. Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York, pp 296–314

Standovár T, Kenderes K (2003) A review on natural stand dynamics in Beechwods of East Central Europe. Appl Ecol Environ Res 1:19–46

Tabaku V (2000) Struktur von Buchen-Urwäldern in Albanien im Vergleich mit deutschen Buchen Naturwaldreservaten und Wirtschaftswäldern. Cuvillier Verlag, Göttingen

Tesař V, Krečmer V (2001) Search for a balance between changing requirements for benefits from the forest and its condition in the Moravian-Silesian Beskids (Czech Republic). Schweiz Z Forstwes 152:145–151

Tolasz R, Míková T, Valeriánová A, Voženílek V (2007) Climate atlas of Czechia. Český hydrometeorologicky ústav a Univerzita Palackého v Olomouci, Prague-Olomouc

Unar P, Šamonil P (2008) The evolution of natural floodplain forests in South Moravia between 1973 and 2005. J For Sci 54:340–354

Vandekerkhove K, De Keersmaeker L, Menke N, Meyer P, Verschelde P (2009) When nature takes over from man: dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. For Ecol Manag 258:425–435

Vandekerkhove K, De Keersmaeker L, Walleyn R, Kohler F, Crevecoeur L, Govaere L, Thomaes A, Verheyen K (2011) Reappearance of old-growth elements in lowland woodlands in northern Belgium: do the associated species follow? Silva Fenn 45:909–935

Vrška T, Adam D, Hort L, Odehnalova P, Horal D, Kral K (2006) Developmental dynamics of virgin forest reserves in the Czech Republic II—Floodplain forests—Cahnov-Soutok, Ranšpurk, Jiřina. Academia, Prague

Vrška T, Adam D, Hort L, Kolář T, Janík D (2009) European beech (*Fagus sylvatica* L.) and silver fir (*Abies alba* Mill.) rotation in the Carpathians—a developmental cycle or a linear trend induced by man? For Ecol Manag 258:347–356

Vrška T, Šamonil P, Unar P, Hort L, Adam D, Kral K, Janik D (2012) Developmental dynamics of virgin forest reserves in the Czech Republic III—Šumava Mts. and Český les Mts.—Diana, Stožec, Boubín virgin forests, Milešice virgin forest. Academia, Prague

Watt AS (1947) Pattern and process in the plant community. J Ecol 35:1–22

Wiens JA (1995) Landscape mosaics and ecological theory. In: Hansson L, Fahrig L, Merriam G (eds) Mosaic landscapes and ecological processes. Springer, Dordrecht, pp 1–26. doi:10.1007/978-94-011-0717-4_1

Winter S, Brambach F (2011) Determination of a common forest life cycle assessment method for biodiversity evaluation. For Ecol Manag 262:2120–2132

Worrall JJ, Lee TD, Harrington TC (2005) Forest dynamics and agents that initiate and expand canopy gaps in Picea–Abies forests of Crawford Notch, New Hampshire, USA. J Ecol 93:178–190

Zang R, Tao J, Li C (2005) Within community patch dynamics in a tropical montane rain forest of Hainan Island. South China Acta Oecologica 28:39–48

Zukrigl K, Eckhardt G, Nather J (1963) Standortskundliche und waldbauliche Untersuchungen in Urwaldresten der nielderösterreichischen Kalkalpen. Mitteilungen Forst Bundesversuchanstalt 62:1–244