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A demographic equilibrium approach to stocking control in mixed, multiaged stands in Bialowieża Forest, northeast Poland

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ABSTRACT

Manifold benefits and advantages of mixed tree stands have been known for many decades. However, while developing and maintaining multiaged and mixed-species forests with complex stand structures has often been advocated and has recently become a worldwide priority, it is not a simple task. One important reason for this is a lack of appropriate methods for controlling long-term development of such stands. Here, we present a possible solution for this problem by applying the demographic equilibrium approach to guide stocking and structure regulation in mixed stands. We tested the practical usefulness of this approach using permanent-plot inventories from 2002, 2011 and 2018, in mixed tree stands in the Experimental Sustainability Unit (ESU) Browsk 28C, in the managed part of Białowieża Forest (NE Poland). For our analysis, ESU Browsk 28C (about 30 ha) was treated as a silvicultural planning unit. First, on the basis of target stand types defined in Polish Silvicultural Guidelines (2012) and forest sites occurring at the study site, desirable tree species composition was determined. Eleven tree species of varying life histories and ecological attributes were included: aspen, birch, alder, pine, oak, maple, ash, elm, spruce, lime, and hornbeam. In the second step equilibrium diameter distributions were constructed for each species, taking into account species-specific growth and mortality rates, as well as targeted proportional representation. Next, theoretical species-specific equilibrium diameter distributions were visually and quantitatively compared with empirical distributions from permanent sample plots. Finally, departures of empirical from theoretical distributions served as a basis for silvicultural recommendations and prescriptions. We prioritized silvicultural measures (such as patch cuts opening larger gaps in forest canopy, proper site treatment, planting, protection against browsing by large herbivores), promoting compositionally diverse forest reproduction and recruitment as essential to long-term maintenance of demographic sustainability in mixed forest stands. We conclude that the demographic equilibrium approach is particularly valuable for creating and maintaining complex forest structures in multi-species stands.

1. Introduction

Silvicultural practice has long made a fundamental distinction between pure and mixed stands (Dengler, 1944; Oliver and Larson, 1996; Aston and Kelty, 2018). Although manifold benefits and advantages of mixed tree stands have been recognized for many decades (Gayer, 1886), forestry practice in many parts of the world, and particularly in Central Europe, has strongly favored the establishment and management of pure stands (Bartelink and Olsthoorn, 1999; Pretzsch and Zenner, 2017). Recently, priorities have changed and there is a critical need to create and maintain mixed-species and multiaged forests (Duchiron, 2000; Schütz, 2001, 2002; Franklin et al., 2002; Spiecker, 2003; Pretzsch et al., 2008; Bauhus et al., 2009; Brzeziecki et al., 2013; Brang et al., 2014; O'Hara, 2014, 2016; Bravo-Oviedo et al., 2018; Ammer, 2019; Steckel et al., 2020). However, developing and maintaining forests with complex stand structures is not a simple exercise, and silviculturalists lack tools and methods enabling stocking control and long-term developmental regulation of mixed-species, structurally diverse forest stands (Coll et al., 2018; Bravo et al., 2019). After O'Hara (2014), stocking control or stocking regulation can be defined as practices controlling the density, species composition, and sizes of trees through periodic harvest treatments, thinnings, and regeneration treatments.

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These treatments or operations serve to reallocate growing space (often expressed as stand basal area per hectare) within the stand. In other words, stocking control provides guidance for harvest treatments, consistent target stand structures, and long-term stability (O'Hara 2014). Traditionally, stocking control guidelines have represented stand structure through measures such as stand density or diameter distributions (O'Hara, 2014; Río et al., 2016; Pretzsch and del Río, 2020). While particular stand density indices (like Reineke's Stand Density Index; cf. Bravo-Oviedo et al., 2014) are appropriate for even-aged, usually mono-species stands, measures based on diameter distributions are a more common approach when structurally diverse, multiaged (uneven-aged) tree stands are the management goal (O'Hara and Gersonde, 2004; O'Hara, 2014). The use of different types of diameter distributions determining target size (and age) structure for complex forest stands has a long tradition in forestry, indeed. Important examples include a reverse J-shaped diameter distribution (De Liocourt, 1898), negative exponential distribution (Meyer and Stevenson, 1943; Meyer, 1952; Leak, 1964; Goodburn and Lorimer, 1999; Sterba, 2004), rotated sigmoid distribution (Goff and West, 1975; Lorimer and Frelich, 1984), the BDq system (q-factor approach) (Cancino and von Gadow, 2002; O'Hara and Gersonde, 2004), and demographic equilibrium approach (Schütz, 1975, 1997, 2001, 2006).

Targeting desired demographic structures is particularly valuable in management of mixed, uneven-aged stands. In comparison to other, mostly descriptive and static methods, the demographic approach takes explicitly into consideration two fundamental population processes - species-specific, size-dependent growth and mortality - which jointly determine the shape of tree size distributions at the equilibrium state (Borel, 1929; François, 1938; Prodan, 1949; Schütz, 1975, 2006; Harcombe, 1987; Condit et al., 1998; Schütz and Pommerenning, 2013). Thus, applying a demographic approach makes it possible to account for species differences in mortality rates and growth patterns, which are particularly important in the dynamics of mixed forest stands.

So far, the demographic approach has most often been used to assess demographic balance of species in unmanaged (natural, old-growth) forest systems (Coomes et al., 2003; Wang et al., 2009; Salk et al., 2011; Brzeziecki et al., 2016). Although the examples exist for managed forests, they usually concern stands with strong single-species dominance (Schütz, 2001, 2006; Schütz and Pommerenning, 2013). In contrast to previous applications, we explore the potential of the demographic approach as a management tool in mixed, structurally diverse forest stands, consisting of a relatively large number of ecologically different tree species. To test the practical value and usefulness of this approach, we use empirical stand data, collected between 2002 and 2018 on permanent plots in a pre-defined silvicultural planning unit (about 30 ha), located in the managed part of Białowieża Forest in NE-Poland.

2. Materials and methods

2.1. Study area and study site

Białowieża Forest is situated on both sides of the national border between Poland and Belarus. It encompasses in total 1455 km^2 (605 km^2 in Poland and 850 km^2 in adjacent Belarus). The climate has features of both Continental and Atlantic character (Faliński, 1986). Average annual temperature is 7.0 °C (January average = -4.6 °C, July average = 18.2 °C), total annual precipitation averages 631 mm and snow cover lasts for an average of 92 days (Faliński, 1986). Białowieża Forest is situated on a flat, undulating terrain ranging from 135 to 190 m a.s.l., built from glaciofluvial sands, gravels and clays (Kwiatkowski, 1994). The Polish section of Białowieża Forest is divided into the protected (Białowieża National Park, about 105 km^2) and the managed part (about 500 km^2), which is subdivided into three forest districts: Białowieża, Hajnówka and Browsk.

Empirical data used to check the effectiveness of the demographic equilibrium approach were collected in forest compartment 28C, located in the Browsk Forest District (Appendix 1). The overall size of this compartment is 28.54 ha. The dominant forest site type is fresh broadleaf forest (FBF), which develops on productive, brown soils, with high cation concentrations and pH. Other forest types include fresh mixed broadleaf forest (FMBF), wet broadleaf forest (WBF) and flood-plain forest (FPF) (distinguished after Polish Silvicultural Guidelines (2012); cf. also Appendix 2 and 3). The forest stands occurring in the compartment are relatively young (age of oldest trees is slightly over 100 years) and consist of 11 different tree species (Table 1). Most stands originated after clearcuts executed by German occupation authorities during the First World War (Więcko 1984). The clearcuts were continued in the 1920s by the English company, 'The Century Timber Corporation', acting on the basis of an agreement with the Polish government. Clearcut areas were, in part, artificially regenerated by planting (mainly of Scots pine and pedunculate oak – cf. Fig. 1). Many clearcut areas, however, have regenerated naturally, initially by fast growing, shade intolerant tree species (aspen, birch, alder) and later by more shade tolerant hornbeams, spruces, elms and maples. From the end of the Second World War until recently, the whole compartment has received regular maintenance treatments (cleanings and thinnings) aimed principally at favoring more valuable pine, oak, and spruce over less desirable aspens, birches and hornbeams. About 20 years ago, a form of irregular shelterwood system (Schütz, 2001; Raymond and Bédard, 2017) was introduced over the whole compartment, with the general goal of imitating natural gap dynamics and initiating regeneration of desired species, especially in places dominated by mature and over-mature aspens, birches and hornbeams. Within the management unit, about 20 openings (canopy gaps) were created, with a mean size of 0.15 ha (0.08 to 0.29 ha; in total 3 ha, i.e., about 10% of the whole compartment area), and artificially regenerated by planting oak seedlings, supplemented by natural regeneration largely of maples, elms, hornbeams, birches and aspens. All regeneration patches were fenced to protect young trees against browsing by ungulates. Meanwhile, in the remaining parts of stands, single and group cuttings were carried out, intended to favour oak, pine, spruce, elm and maple trees and to harvest mature individuals of birch, aspen, alder and hornbeam. Also, nearly every year, salvage cuttings removed spruce trees attacked by bark beetles.

In 2002 the Experimental Sustainability Unit (ESU) was established within compartment 28C (Brzeziecki et al., 2013). It was intended to serve as a test site for developing unconventional silvicultural approaches aimed at creating multiple-benefit forests, simultaneously serving wood production, recreation, and nature conservation goals.

Table 1
A list of tree species occurring in ESU Browsk 28C. The sequence of species corresponds to their relative position along a major environmental gradient from most oligotrophic to most eutrophic sites. DST – degree of shade tolerance (after Brzeziecki et al., 2016).

No	Tree species	Scientific name	DST
1	Pine	*Pinus sylvestris* L.	Intolerant
2	Birch	*Betula* sp.[1]	Intolerant
3	Aspen	*Populus tremula* L.	Intolerant
4	Oak	*Quercus robur* L.	Intermediate
5	Spruce	*Picea abies* (L.) Karst.	Tolerant
6	Hornbeam	*Carpinus betulus* L.	Tolerant
7	Lime	*Tilia cordata* Mill.	Tolerant
8	Maple	*Acer platanoides* L.	Intermediate
9	Elm	*Ulmus* sp.[2]	Intermediate
10	Ash	*Fraxinus excelsior* L.	Intermediate
11	Alder	*Alnus glutinosa* (L.) Gaertn.	Intolerant

[1] – *Betula pendula* Roth. & *B. pubescens* Ehrh. (predominantly *B. pendula*).
[2] – *Ulmus glabra* Hudson, *U. laevis* Pallas & *U. minor* Mill. (predominantly *U. glabra*).

Fig. 1. Approximately 90-year old, high-quality oak trees (labeled by letter 'O') growing in ESU Browsk 28C. Oaks were artificially regenerated (planted) after clearcuttings, protected against browsing by ungulates and continuously supported by silvicultural treatments (cleanings and thinnings). Other tree species (mainly hornbeam and spruce) regenerated naturally.

2.2. Field data collection

In 2002, 25 permanent, nested, circular, 0.05 ha sample plots were established, in a regular 100 m × 100 m grid, for a first stand inventory of the ESU Browsk 28C (Appendix 2). Every sample plot consisted of 5 nested subplots. The smallest three subplots ('regeneration' plots; 1–3) were used for inventory of tree regeneration, classified into three developmental classes. The remaining two subplots ('stand' plots) were used for inventory of adult trees (DBH ≥ 7 cm and ≥ 35 cm for subplots 4 and 5, respectively) (Table 2).

In 2011 and 2018, successive inventories of ESU Browsk 28C used the same methodology. In addition, in the repeated inventories, 'losses' (mortality due to natural causes or harvest) and 'recruits' (trees reaching minimum DBH (diameter at the breast height) threshold value of either 7 cm (within the subplot 4 – so called 'small recruits'), or 35 cm (outside the subplot 4 but within the subplot 5 – so called 'large recruits')) were recorded.

In 2002, stand measurements were performed by means of standard caliper (DBH), compass and laser rangefinder (to establish polar coordinates of trees within plots) and the Vertex III ultrasound hypsometer system (tree heights). During the second and third inventory, the tree measurements were conducted by means of an electronic caliper and Field-Map technology (www.field-map.cz).

At present, tree stands occurring in ESU Browsk 28C are distinguished by a rather high compositional and, to some degree, vertical variation at the scale of sample plots (Fig. 2; cf. also Appendix 4).

2.3. Calculation of basic stand data

Tree density (ha^{-1}), basal area ($m^2 \cdot ha^{-1}$) and merchantable tree volume (over bark) ($m^3 \cdot ha^{-1}$) were calculated, in total and by species, for all sample plots and each inventory date, for trees with DBH ≥ 7 cm. Stand-level means and confidence intervals were determined for these parameters.

A periodic annual volume increment ($PAVI_{t1\text{-}t2}$, $m^3 \cdot ha^{-1} \cdot year^{-1}$) was computed by the formula suggested by Mięcicki and Nowicka (2008) for permanent, nested sample plots:

$$PAVI_{t1-t2} = \left(V_{t2} - V_{t1} - R_{7;t1-t2} - R_{35;t1-t2} + OG_{t1-t2} + M_{t1-t2}\right)/L \qquad (1)$$

where:

$PAVI_{t1\text{-}t2}$ – annual volume increment ($m^3 \cdot ha^{-1} \cdot year^{-1}$), in the period t_1–t_2;

V_{t1}, V_{t2} – stand volume ($m^3 \cdot ha^{-1}$) at the beginning (t_1) and the end (t_2) of inventory period;

Table 2
Range of measurements conducted on five nested sample plots.

Subplot number	1	2	3	4	5
Radius (m)	1.26	2.52	3.99	7.98	12.62
Area (m^2)	5	20	50	200	500
Range of measurements	Age ≥ 2 years and h < 0.5 *m*	h ≥ 0.5 m and DBH < 2 cm	DBH ≥ 2 cm and DBH < 7 cm	DBH ≥ 7 cm and DBH < 35 cm	DBH ≥ 35 cm
Stratum	Seedlings	Small saplings	Tall saplings	Stand 1	Stand 2
Parameters	Species, density, vigour (4 classes)	Species, density, vigour (4 classes)	Species, density, vigour (4 classes)	Species, DBH, height[1], polar coordinates, stem quality (4 classes)	Species, DBH, height[1], polar coordinates, stem quality (4 classes)

[1] measured for selected trees only (usually two individuals per species on the plot).

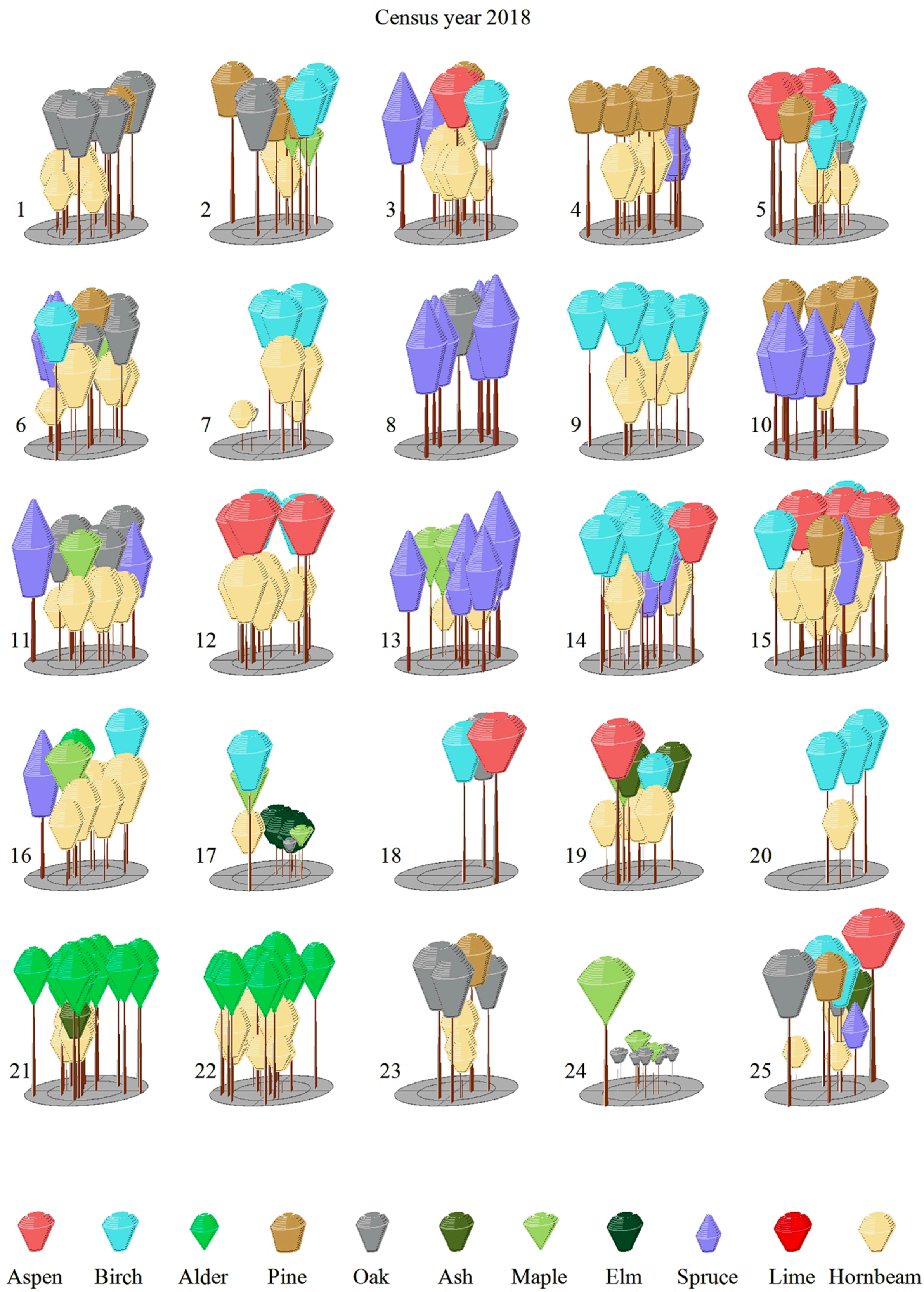

Fig. 2. Compositional and structural variation of tree stands occurring in ESU Browsk 28C, as represented by 25 permanent, circular sample plots (Appendix 2). Census date: 2018. Only live trees with DBH ≥ 7 cm (0.02 ha subplot) and with DBH ≥ 35 cm (0.05 ha subplot) are shown. Scientific names of tree species are provided in Table 1.

$R_{7;t1\text{-}t2}$ – volume of 'small recruits' (multiplied by 50 = 10,000/200) ($m^3 \cdot ha^{-1}$) – trees which reached a threshold of 7 cm DBH at the end of inventory period (t_2) – measured within a smaller 'stand' plot (area = 200 m^2);

$R_{35;t1\text{-}t2}$ – volume of 'large recruits' (multiplied by 20 = 10,000/500) ($m^3 \cdot ha^{-1}$) – trees which reached a threshold of 35 cm DBH at the end of inventory period (t_2) – measured outside a smaller 'stand' plot, but within a larger 'stand' plot (area = 500 m^2):

$OG_{t1\text{-}t2}$ – volume of trees which in the period t_1–t_2 exceeded the threshold of 35 cm within the smaller 'stand' plot; calculated by subtracting their volume at t_2 (multiplied by 20) from their volume at t_1 (multiplied by 50) ($m^3 \cdot ha^{-1}$);

$M_{t1\text{-}t2}$ – volume of trees which died naturally or were harvested during the inventory period t_1–t_2 ($m^3 \cdot ha^{-1}$);

L – length of inventory period (years).

The calculation of volume increment was performed separately for two inventory periods: 2002–2011 and 2011–2018.

We also determined density and species composition of regeneration (seedlings and saplings), as well as number of recruits by species for the two inventory periods. All calculations were performed in the Field-Map Inventory Analyst module (www.fieldmap.cz), supported by the R statistical computing environment (R Core Team, 2019).

2.4. Target tree species allocations in ESU Browsk 28C

Target (desirable) percentage shares (expressed in terms of basal area) of tree species for ESU Browsk 28C were calculated using a two-step approach. First, the percentages of tree species for every forest site type occurring in ESU were determined, on the basis of target stand types provided in Polish Silvicultural Guidelines (2012) for the Białowieża Forest region. These target stand types included the so called *major* tree species (primarily responsible for forest production) and *minor* tree species (contributing to non-productive functions of forest (e.g., relating to biodiversity)). Second, the overall, averaged percentages of particular species in the entire ESU were calculated, weighted by area of a given site type. Finally, the values of species-specific basal area were calculated, by assuming that the total stand basal area in ESU amounts to 30 $m^2 \cdot ha^{-1}$. This figure was chosen rather arbitrarily as an approximation of current basal area for all stands across the ESU (Tables 3 and 5).

2.5. Equilibrium, species-specific diameter distributions

Under the demographic approach, long-term sustainability of forest stands and tree populations is determined by a simple rule; over time, the number of trees moving into a given size/diameter class through growth (in-growth) must equal the number of trees leaving that size class due to growth (out-growth) or mortality due to natural causes or management (Schütz, 2006). In accordance with this rule, to determine species-specific equilibrium diameter distributions, the following formula was used (Brzeziecki et al., 2016; cf. also: Lorimer and Frelich, 1984; Schütz, 2006; Salk et al., 2011):

$$n_{i+1} = (1 - l_i)\cdot n_i \cdot p_i / ((1 - l_{i+1})\cdot p_{i+1} + l_{i+1}) \tag{2}$$

where:

n_i, n_{i+1} – the numbers of trees in diameter classes i and $i + 1$, respectively;

p_i, p_{i+1} – the outgrowth rates, i.e. proportions of trees moving from diameter class i to class $i + 1$ and from diameter class $i + 1$ to class $i + 2$, respectively, during a given period;

l_i, l_{i+1} – the mortality rates, i.e. the proportions of trees in diameter classes i and $i + 1$, respectively, which died or were harvested during the same period.

The outgrowth rate p was determined by multiplying the annual absolute diameter growth rate g by the length of the corresponding census period Δt and dividing by the diameter class width (4-cm diameter classes were used). The absolute diameter growth rate g itself was estimated by means of the first derivative of the Chapman-Richards growth function using DBH instead of time (Brzeziecki et al., 2016). The species-specific mortality rate l was estimated using a binary logistic function. Both natural mortality and growth functions were parameterized using empirical data from permanent study plots established in Białowieża National Park and surveyed over the period 1936–2012 (cf. Appendix S9 in Brzeziecki et al., 2016). The reduction terms (1–l_i and 1–l_{i+1}) in formula (2) were introduced by Brzeziecki et al. (2016) to account for the mortality of trees which moved out of classes i and $i + 1$ during the observation period, but then died before the end of that period.

The calculation of tree number in consecutive diameter classes was performed starting always from n_1 (number of trees in the first, smallest diameter class). The value of n_1 was determined by a trial and error method such that the resulting equilibrium basal area amounted to the desirable (target) basal area of a given species in ESU.

After establishing the steady-state distributions, for each tree species, a theoretical number of recruits (R_{mod}) was determined by means of the following formula (Brzeziecki et al., 2016):

$$R_{mod} = n_1 \cdot p_1 + n_1 \cdot l_1 \tag{3}$$

where n_1, p_1 and l_1 are the number of trees, the outgrowth rate and the loss rate in the smallest diameter class, respectively. The theoretical recruitment rates for all species were compared with observed recruitment rates for the two census periods.

To evaluate the departure of empirical, species-specific tree-size distributions from theoretical equilibrium curves, the absolute discrepancy was calculated (Westphal et al., 2006):

$$d = \frac{1}{2}\sum_{j=1}^{n}\left|\widehat{x}_i - x_i\right| \tag{4}$$

where n is the number of diameter classes, and $\widehat{x}_i$ and x_i are the relative frequencies of trees in classes of the theoretical (estimated) and empirical distributions.

The absolute discrepancy d is equal to the proportion of the diameter frequencies which has to be exchanged so that the observed empirical distribution is exactly equal to the theoretical (equilibrium) distribution. The distributions are identical for $d = 0$; they have nothing in common for $d = 1$.

Table 3
Main parameters (means and confidence intervals for $\alpha = 0.05$) of tree stands occurring in the ESU Browsk 28C, for subsequent census dates: n – number of sample plots; N – density ($1 \cdot ha^{-1}$) (for trees with DBH ≥ 7 cm); BA – stand basal area ($m^2 \cdot ha^{-1}$); V_{ob} – merchantable stand volume over bark ($m^3 \cdot ha^{-1}$).

Year	n	N	BA	V_{ob}
2002	25	684 ± 111	30.2 ± 3.0	377.0 ± 57.7
2011	25	558 ± 104	29.1 ± 4.7	375.6 ± 61.0
2018	25	522 ± 84	30.4 ± 4.8	404.7 ± 64.9

Table 4
Periodic annual volume increment over bark ($PAVI$, $m^3 \cdot ha^{-1} \cdot year^{-1}$) and its main components: V_{ob} – merchantable stand volume over bark ($m^3 \cdot ha^{-1}$); R_7 and R_{35} - volume of 'small' and 'large' recruits, respectively ($m^3 \cdot ha^{-1}$); OG - volume of trees which exceeded the threshold of 35 cm within the smaller 'stand' plot ($m^3 \cdot ha^{-1}$); M - volume of trees which were harvested or died during the study period ($m^3 \cdot ha^{-1}$). L – length of increment period (years).

Census date	L	$PAVI$	V_{ob}	R_7	R_{35}	OG	M
2002	9	9.9	377.0	–	–	–	89.1
2011			375.6	0.4	18.9	24.8	–
2011	7	9.4	375.6	–	–	–	65.9
2018			404.7	0.7	11.4	7.7	–

Table 5
Percentage share of tree species in particular forest site types (determined after Polish Silvicultural Guidelines (2012)) and total target share (*MOD*, %; calculated as an arithmetical average weighted by an area of a given forest type) of tree species in ESU Browsk 28C. BA_T and BA_E – theoretical and empirical basal area of tree species ($m^2 \cdot ha^{-1}$), respectively.

Tree species	Forest site types[1] and their percentage share (%) in the ESU Browsk 28C					*MOD*	BA_T	BA_E^2
	FMBF (16)	WMBF (1)	FBF (73)	WBF (7)	FPF (3)			
Oak	30	30	40	20	0	35	10.7	3.9
Spruce	20	20	20	20	10	20	5.9	4.5
Pine	20	10	10	0	0	11	3.2	4.0
Hornbeam	10	10	10	10	10	10	3.0	4.9
Lime	0	0	10	10	10	8	2.5	0.0
Maple	0	0	10	10	0	8	2.4	1.4
Alder	0	10	0	10	40	2	0.6	3.1
Birch	10	10	0	0	10	2	0.6	4.8
Aspen	10	10	0	0	0	2	0.5	3.1
Elm	0	0	0	10	10	1	0.3	0.2
Ash	0	0	0	10	10	1	0.3	0.5
Total	100	100	100	100	100	100	30.0	30.4

[1] – FMBF – fresh mixed broadleaf forest; WMBF – wet mixed broadleaf forest; FBF – fresh broadleaf forest; WBF – wet broadleaf forest; FPF – flood plain forest; cf. also Appendix 2 and Appendix 3; [2] – values determined during 2018 census.

3. Results

3.1. Basic stand parameters

Between 2002 and 2018, the overall tree density, for all stands occurring in ESU Browsk 28C, decreased by about 24%, while stand volume increased by about 7%. At the same time, the total stand basal area remained relatively stable (Table 3). Periodic annual volume increment over bark was comparable in two census periods and amounted to about 9–10 $m^3 \cdot ha^{-1} \cdot year^{-1}$ (Table 4).

3.2. Target tree species allocations in ESU Browsk 28C

Target stand types, defined after Polish Silvicultural Guidelines (2012) for forest sites occurring in ESU Browsk 28C, included eleven different tree species (Table 5). The overall model share of a given tree species (column *MOD*) depended on its assumed 'role' in a particular forest site category and on the percentage share of this category in ESU. The most important (*major*) tree species were oak, spruce, pine, hornbeam, lime and maple (with individual shares ≥ 8%). Alder, birch, aspen, ash and elm formed a group of *minor* species (with individual shares ≤ 2%). Observed basal areas of most tree species (column BA_E) deviated, to a smaller or larger extent, from theoretical (model, desirable) values (column BA_T) (Table 5).

3.3. Empirical species-specific diameter distributions and their comparison with theoretical demographic equilibrium curves

Occurrences of most tree species were limited to some segments of the overall DBH range (Fig. 3a). In the smallest DBH classes, hornbeam was dominant while the largest DBH classes were occupied mainly by aspen trees. Remaining tree species were confined largely to intermediate DBH classes. In contrast to actual distributions, in theoretical target distributions, most tree species were represented more or less evenly over most of the DBH range (Fig. 3b).

Empirical diameter distributions for the six *major* tree species (oak, spruce, pine, hornbeam, lime and maple), diverged variably from theoretical, sustainable distributions (Fig. 4a). For example, the current population structure of oak, the most important tree species in ESU according to the allocation model (Table 5), deviated from the theoretical distribution, both negatively and positively. Intermediate diameter classes (25 to 41 cm) were over-represented while both the smallest (<25 cm) and the largest (>57 cm) DBH classes were under-represented. Over the entire study period (2002–2018), important changes in oak demographic structure occurred. Rapid diameter growth caused several oak trees to move from 25 into 33 cm DBH class. Moreover, during the second observation period (2011–2018), oak density in the first diameter class (9 cm) increased significantly. In case of spruce, the second important tree species in ESU stands, only the 45 and 49 cm DBH classes in the last survey showed over-representation compared to the theoretical model. For most size classes, deficits prevailed and increased over time, particularly in the two smallest diameter classes (9 and 13 cm). Regarding small trees, a similarly undesirable result was also found for Scots pine. Deficits in pine population occurred over the wide range of DBH classes (from 9 to 25 cm) and increased over time. Unlike spruce, however, in pine population, there were some surplus trees in larger diameter classes (33 cm and 41 cm). Hornbeam's observed population structure was quite different compared to the previous three species. Over the entire observation period, densities of small hornbeam trees (DBH classes from 9 to 25 cm) were much higher than the calculated model values, even after decreases from 2002 to 2018 in hornbeam numbers in the two smallest DBH classes. On the other hand, there was a deficit of hornbeams in DBH classes 33 cm and larger. Lime, although included in target species composition, was totally missing in ESU Browsk 28C (at least for DBH ≥ 7). The final *major* tree species, maple, exhibited demographic status relatively close to the target composition (similarly to oak). The biggest deficiencies occurred for maple trees larger than 37 cm. As with oak, during the second observation period, there was a notable increase of maple trees in the smallest diameter class (9 cm).

Among *minor* tree species, alder, birch and aspen were most important. They all represented a group of fast growing, shade intolerant tree species (Table 1) and their current demographic status was rather similar (Fig. 4b). All exhibited large surpluses of stems either in intermediate (alder and birch) or large (aspen) size classes. At the same time, all these species exhibited large deficits in small diameter classes. Other *minor* species were elm and ash. The demographic status of ash was slightly better than that of elm, even though ash population density declined substantially during the entire observation period. Relative over-representation for selected diameter classes for both elm and ash were mainly the result of their rather small shares in the assumed target species composition.

Overall empirical distributions, obtained by summing all species, corresponded relatively closely to the corresponding theoretical model for all census dates (Fig. 4b, 'Total'). This effect contrasts to results for individual species, where observed distributions departed substantially from theoretical curves, and suggests some alignment of discrepancies, observed at the species level, when the entire stand level is considered.

Calculated discrepancy (*d*) values, measuring similarity between theoretical and empirical distributions (Table 6), suggest that species

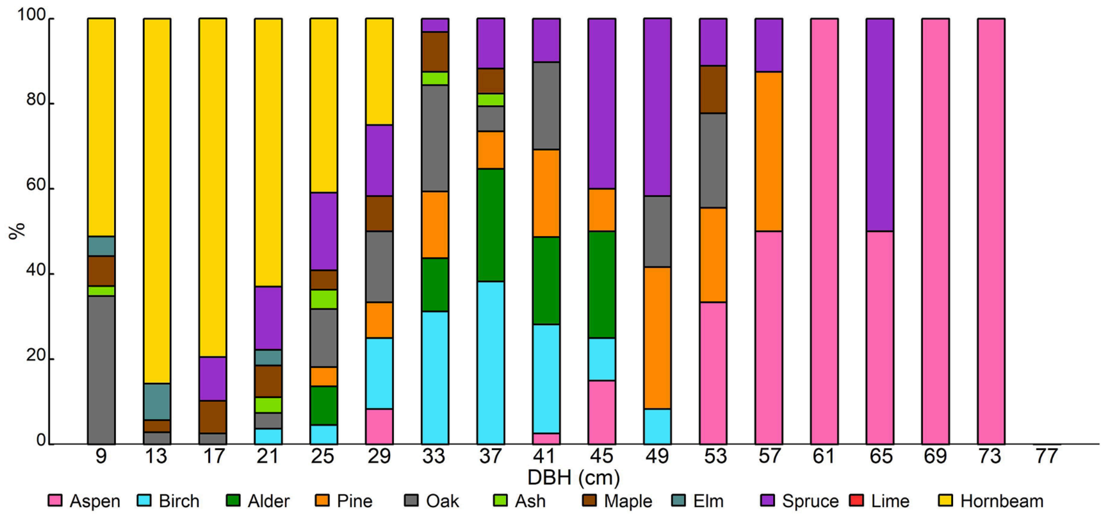

Fig. 3a. Actual distribution of relative tree numbers, by species, in particular diameter classes in the ESU Browsk 28C (obtained on the basis of empirical diameter distributions as determined during 2018 census). Scientific names of tree species are provided in Table 1.

may be assigned to two major groups. One group, consisting of oak, hornbeam, maple, elm and ash, was characterized by a relatively high similarity between empirical and theoretical distributions (the values of discrepancy coefficients were between 0.3 and 0.5). The second group contained remaining tree species, for which values of *d* generally ranged from 0.7 to 1.0. Value of *d* for overall, stand-level diameter distribution was relatively small (about 0.2).

Differences between theoretical and empirical densities, calculated for three major size categories (small, medium and large trees), revealed a characteristic pattern (Table 6). Most species exhibited deficits of small and large trees. The only noticeable exception was hornbeam, for which small trees were over-represented relative to demographic equilibrium predictions. In contrast to small and large trees, the category of medium trees was distinguished by presence of many surplus trees. The largest surpluses were exhibited by hornbeams, birches and alders.

Comparison between theoretical model and observed distribution for all species pooled shows that biggest deficiencies occurred for the smallest DBH classes (9 and 13 cm) (Fig. 5). Simultaneously, in the middle DBH range (17 to 45 cm) actual numbers of trees exceeded, to variable degree, theoretical values.

3.4. Regeneration and recruitment

In spite of some variation between census dates, data on the tree regeneration layer revealed some general, persistent patterns (Table 7). First, tree density shows large decreases from smaller to larger classes, suggesting rather high mortality rates, especially during seedling and small saplings stages. As a consequence, density of large saplings (trees with DBH between 2 and 7 cm) was only about 1% of initial seedling density. A similar tendency applied for the number of tree species in each size class; the seedling layer showed highest species diversity, containing the majority of tree species present as mature individuals in the ESU Browsk 28C. The quantitative role of particular species in ongoing regeneration processes was quite variable. The seedling stage was strongly dominated by maple, hornbeam and aspen in the first census date. Hornbeam also constituted a high proportion of larger regeneration layers (small and large saplings). Other tree species occurred, as a rule, much less abundantly in regeneration classes. However, a high share of oak in the pool of large saplings during the second and third census dates is worth noting. Two species (Scots pine and alder) were completely absent in the regeneration layer.

The recruitment process was dominated by hornbeam (during the

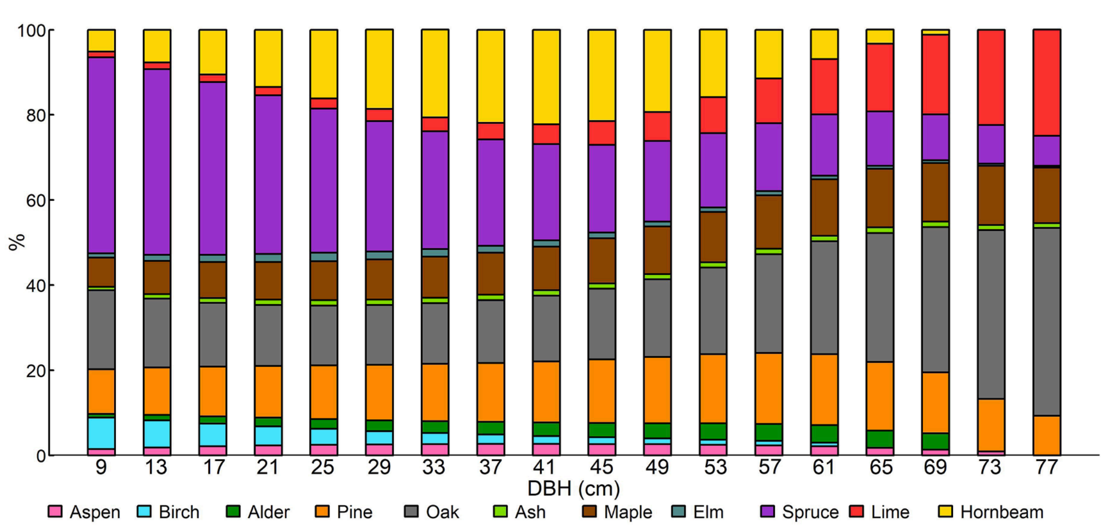

Fig. 3b. Theoretical, target distribution of relative tree numbers, by species, in particular DBH classes (obtained on the basis of theoretical species-specific equilibrium distributions). Scientific names of tree species are provided in Table 1.

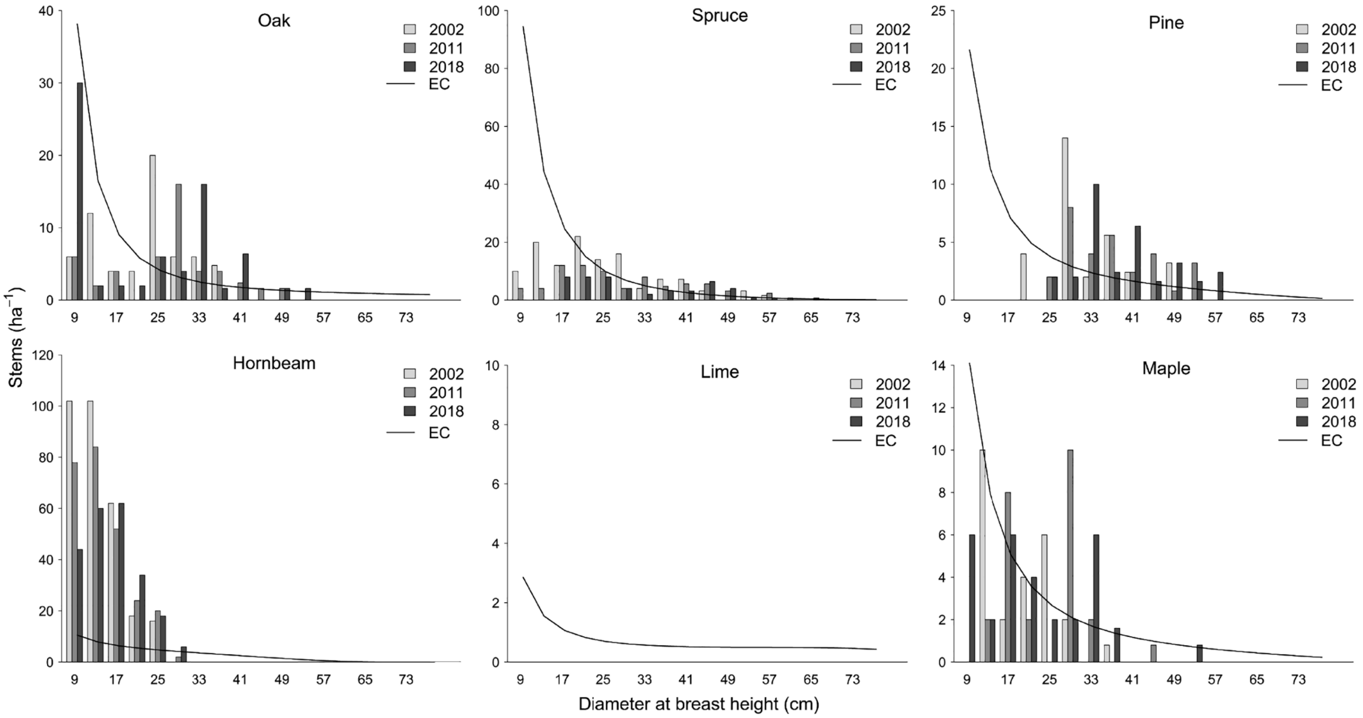

Fig. 4a. Comparison of species-specific empirical tree diameter distributions, as determined for three census dates, with theoretical equilibrium curves (EC). Part 1. *Major* tree species. Scientific names of tree species are provided in Table 1.

first census interval) and oak (during the second census interval) (Table 7). Other species advancing from regeneration to stand layer were elm, spruce, maple and ash. During the second intercensus interval species composition of recruits was more diverse (5 species) than during the first interval (3 species).

In most cases, the observed recruitment rates were smaller than the calculated theoretical values needed to maintain long-term population stability (Fig. 6). Two major exceptions were hornbeam and elm with observed recruitment rates exceeding the theoretical values in both intercensus periods. During the second period, recruitment rates for oak, maple and ash also approached or surpassed the model values.

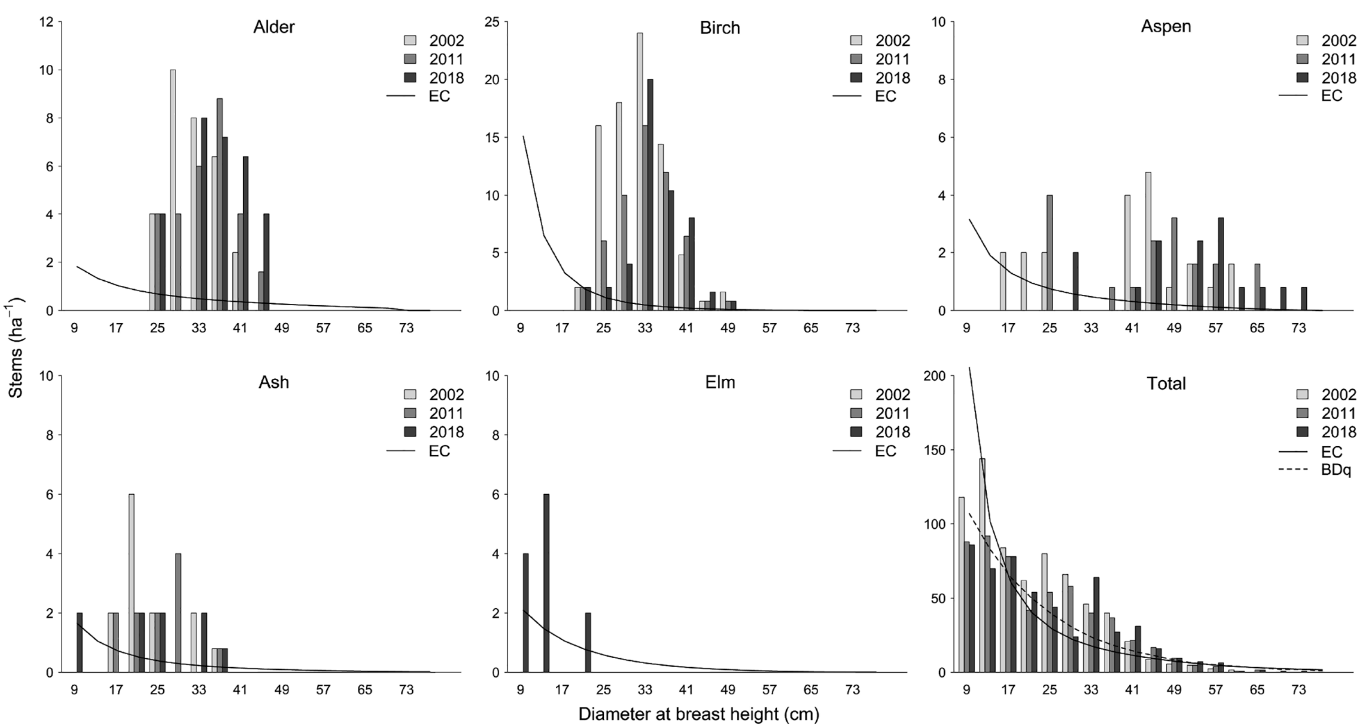

Fig. 4b. Comparison of empirical tree diameter distributions, as determined for three census dates, with theoretical equilibrium curves (EC). Part 2. *Minor* tree species and all species together. For all species, model diameter distribution obtained by means of BDq method is shown, as well (Brzeziecki et al., 2013). Scientific names of tree species are provided in Table 1.

Table 6
Discrepancy (*d*; Eq. (4)) values describing the difference between theoretical (equilibrium) and observed tree distributions, as determined for 2018 census. Densities ($1 \cdot ha^{-1}$) of surplus (*Sur*) and deficit (*Def*) trees, for three size categories: small trees (DBH classes 9 to 21 cm), medium trees (DBH classes 25 to 57 cm), and large trees (DBH classes ≥ 61 cm). Scientific names of tree species are provided in Table 1.

Tree species	*d*	Small trees		Medium trees		Large trees	
		Sur	*Def*	*Sur*	*Def*	*Sur*	*Def*
Oak	0.34	–	22.6	7.8	–	–	4.4
Spruce	0.66	–	138.9	7.9	23.6	–	0.7
Pine	0.74	–	32.9	3.0	–	–	1.9
Hornbeam	0.33	85.6	–	85.5	–	–	0.4
Lime	1.00	–	4.4	–	6.8	–	2.4
Maple	0.35	–	14.0	1.8	–	–	1.8
Alder	0.75	–	3.2	24.3	–	–	0.4
Birch	0.86	–	21.6	40.6	–	–	0.0
Aspen	0.85	–	5.1	5.4	–	3.0	–
Elm	0.42	6.4	–	–	1.8	–	0.1
Ash	0.54	–	0.7	4.0	–	–	0.2
Total	0.24	92.0	243.3	180.3	32.2	3.0	12.3

4. Discussion

4.1. Allocating growing space between tree species in mixed, multiaged/multi-sized tree stands

Stocking control refers to forest management operations that alter the number and arrangement of trees within a stand (O'Hara and Gersonde, 2004). The major task of stocking control or stocking regulation is to reallocate available growing space within the stand (O'Hara, 2014). If the goal is to create and to sustain mixed, multiaged stands, as is the case for ESU Browsk 28C, the accessible growing space must be divided, firstly, among tree species, and, secondly, among size classes (treated as a surrogate for age classes) (Schütz and Pommerenning, 2013). Our approach to this task involved two major steps.

First, the total available growing space, as expressed in terms of overall stand basal area, was partitioned among tree species (cf. Column BA_T in Table 5). This was done to some extent arbitrarily on the basis of information in Polish Silvicultural Guidelines (2012), where most desirable (enabling maintaining of multifunctional character of forest) target stand types have been defined and described. These stand types take into account several important considerations concerning the choice and the presumed shares/roles of particular tree species, including their most important ecological requirements (particularly in respect to climate and soil conditions), economic importance, biocenotic value etc. It is clear, however, that 'roles' assigned to particular species might be redefined so as to increase the importance of some species, although always at a cost to others. Similarly, the overall value of stand basal area ($30\ m^2 \cdot ha^{-1}$), assumed in this study, has been rather arbitrarily chosen. In this case, we have decided to follow the current, empirical value of this parameter, determined for the stands growing in ESU Browsk 28C. However, in the future, this value might be modified (reduced) to favor regeneration of less tolerant species (O'Hara and Gersonde, 2004; Brzeziecki et al., 2013; Schütz and Pommerenning, 2013). Another important aspect to consider may be a volume increment which is usually strongly related to stand basal area (Kelty et al., 2003; O'Hara and Gersonde, 2004; Cancino and von Gadow, 2002). In ESU Browsk 28C, during both census periods, the values of this parameter were rather high ($9–10\ m^3 \cdot ha^{-1} \cdot year^{-1}$) and it would be advantageous to maintain similar levels of volume increment in the upcoming periods. Thus, we treat the chosen value just as a first approximation and subject to future reconsideration following new information and priorities.

In the second step, the species-specific amount of growing space (measured by species-specific basal area determined in the first step), was re-distributed among diameter (and age) classes. To this end, for every tree species, an appropriate equilibrium diameter distribution, ensuring the long-term maintenance of population sustainability (Schütz and Pommerenning, 2013; Halpin and Lorimer, 2017), was constructed. To determine the species-specific shape of equilibrium curves, we have used size-dependent mortality and growth functions with quantitative parameters obtained from analysis of long-term data for tree species occurring in Białowieża Forest (Brzeziecki et al., 2016). Empirical data sets used to parameterize these growth and mortality functions were gathered in stands which have been subjected to strict protection since about 100 years. Adapting these functions to conditions of managed stands may be somewhat problematical, if growth and mortality patterns in the two categories of stands are different. However, a strong argument for using these functions was the fact that they were calibrated on the basis of truly long-term (collected over the period of about 80 years – Brzeziecki et al., 2016), extensive data sets covering a wide range of tree sizes. Nevertheless, in the future, both growth and mortality functions can be re-parameterized, using data from permanent inventory plots established in ESU Browsk 28C. Considering that the overall management goal for the ESU is to create stand structures which would resemble, to some extent, those of protected, natural forest stands, it may turn out that these new functions will not significantly differ from those which have already been used. Visual comparison of empirical growth data collected on permanent inventory plots established in ESU Browsk 28C with growth functions derived from independent data sets, done for selected tree species, appears to support this finding (Appendix 5).

The results of allocating available growing space among tree species and diameter classes, obtained for stands growing in ESU Browsk 28C, are summarized in Fig. 7. In contrast to Fig. 2, the samples presented in Fig. 7 do not show real existing stands, but illustrate theoretical, model stand structures, corresponding to equilibrium diameter distributions determined for particular tree species (cf. also Fig. 4a, b). While simulating these examples, we have assumed a random occurrence of tree species and tree sizes at the sample plot scale (i.e., either 0.02 ha (for trees with DBH ≥ 7 cm) or 0.05 ha (for trees with DBH ≥ 35 cm)). In

Table 7
Density and species composition of forest regeneration, by census date and developmental class. *S* – number of tree species. Scientific names of tree species are provided in Table 1.

Census date	Developmental class	Density ($1 \cdot ha^{-1}$)	*S*	Species composition
2002	Seedlings	21,120	7	Maple – 42%; Aspen – 33%; Hornbeam – 20%; Birch – 3%; Ash – 2%; Oak – 1%; Spruce – <1%.
	Small saplings	2,300	5	Hornbeam – 66%; Aspen – 30%; Maple – 2%; Ash – 1%; Lime – 1%.
	Large saplings	216	2	Hornbeam – 93%; Spruce – 7%.
	Recruits	–	–	–
2011	Seedlings	28,320	7	Maple – 66%; Hornbeam – 27%; Aspen – 5%; Oak – 1%; Ash – 1%; Spruce – <1%; Birch – <1%.
	Small saplings	2,060	6	Hornbeam – 78%; Maple – 10%; Oak – 8%; Rowan – 3%; Ash – 1%; Birch < 1%.
	Large saplings	320	5	Oak – 50%; Hornbeam – 40%; Elm – 5%; Maple – 3%; Spruce – 3%.
	Recruits	32	3	Hornbeam – 69%; Elm – 25%; Spruce – 6%.
2018	Seedlings	38,480	7	Maple – 60%; Hornbeam – 25%; Aspen – 8%; Ash – 6%; Oak – <1%; Spruce – <1%; Rowan – <1%.
	Small saplings	2,660	6	Hornbeam – 60%; Aspen – 17%; Maple – 14%; Rowan – 4%; Elm – 3%; Ash – 2%.
	Large saplings	368	4	Hornbeam – 48%; Oak – 43%; Maple – 7%; Spruce – 2%.
	Recruits	58	5	Oak – 48%; Hornbeam – 28%; Maple – 14%; Elm – 7%; Ash – 3%.

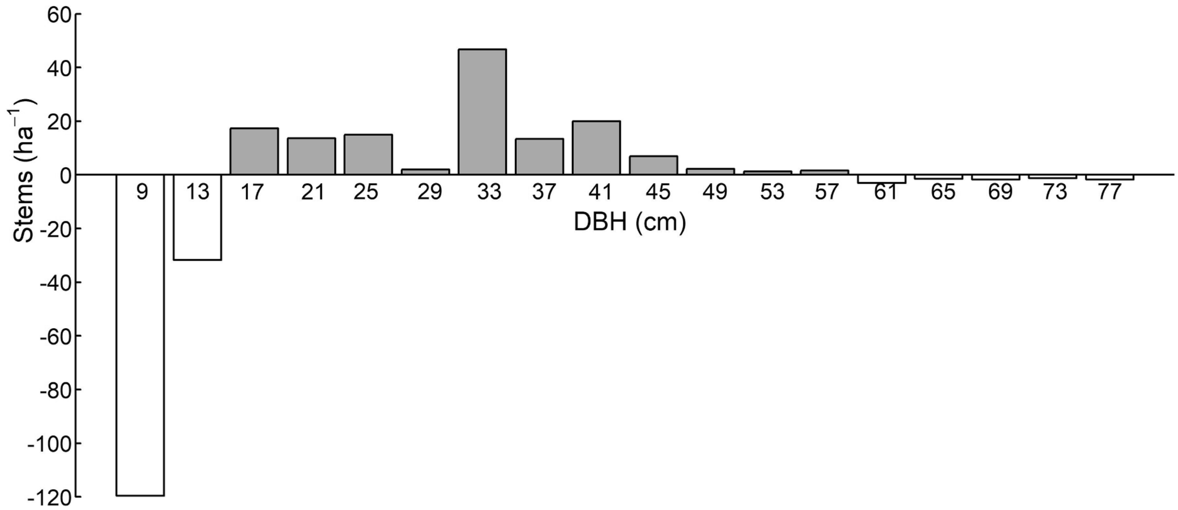

Fig. 5. Deviations between overall equilibrium curve (obtained by totaling the species-specific theoretical distributions) and stand-based empirical diameter distribution (obtained for all tree species).

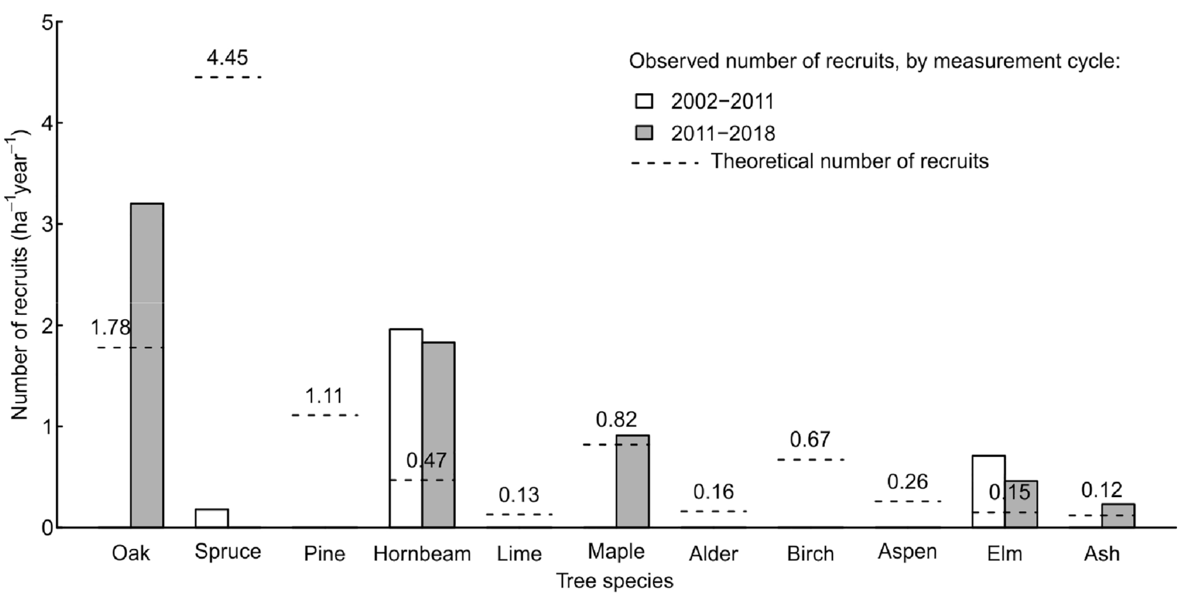

Fig. 6. Observed (bars) vs. theoretical (R_{mod}, Eq. (3); broken lines) number of recruits, among the tree species occurring in ESU Browsk 28C, by survey cycle. Scientific names of tree species are provided in Table 1.

comparison to actual stand structures (Fig. 2), virtual, model stands are distinguished, first, by a much higher differentiation of tree sizes (diameters and heights). Thus, while most forest patches shown in Fig. 2 can be described as two-layered with few shade-tolerant species in the lower canopy and greater diversity in the upper canopy, the examples shown in Fig. 7 present truly mixed and multi-sized stands. In practice, creating and maintaining stand structures as shown in Fig. 7, especially at such small spatial scale, may turn out to be a rather challenging task. However, from the point of view of the silvicultural planning in ESU Browsk 28C, the examples presented in Fig. 7 offer just a general orientation. To maintain long-term population sustainability of particular tree species, it will be crucial (and sufficient) to create their diverse diameter structures at the scale of the whole sustainability unit (in our case ~ 30 ha). In other words, at the patch scale (0.20–0.50 ha), stand structures can be very variable, from relatively simple to very complex; particular patches can vary in tree diversity; they can (and should) also represent different stand growth phases, from regeneration, through young growth, pole stage, mature trees to old growth.

4.2. Discrepancies between theoretical and empirical, species-specific size distributions as a basis for planning silvicultural actions

Comparison of species-specific equilibrium curves to actual diameter distributions illustrates deviations between modeled and actual size distributions. The smaller the deviations, the smaller is the necessity for any silvicultural action. Larger discrepancies require more urgent silvicultural measures aimed at improving the demographic status of a given species and its long-term demographic sustainability. Appropriate measures will depend on the character of discrepancies.

In case of surpluses, when the actual numbers of trees in particular diameter classes exceed the theoretical figures, the problem is relatively simple, calling for appropriate cuttings. Depending on number and volume of surplus trees, this goal can be achieved during a shorter or longer time. One may suggest that the total volume of trees harvested within a given period should not exceed the value of periodic volume increment, determined by means of data collected on permanent inventory plots. In other words, the value of periodic volume increment

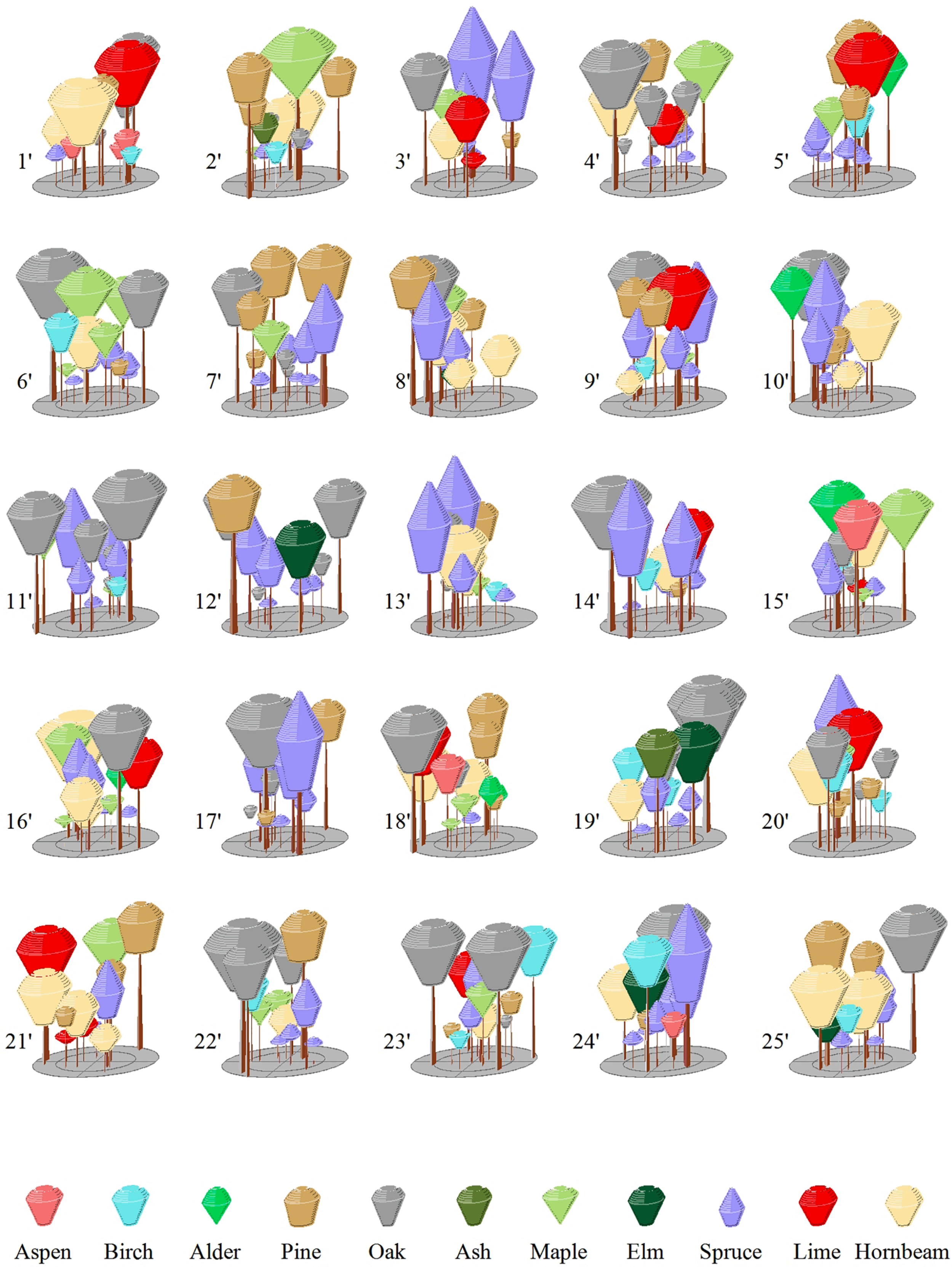

Fig. 7. Virtual, random samples (1′ to 25′) presenting model (target, desirable), mixed-species and multi-sized stand structures, as determined for ESU 'Browsk 28C' on the basis of species-specific equilibrium distributions. Scientific names of tree species are provided in Table 1.

may serve as an additional important parameter to consider when regulating the long-term development of mixed, multiaged stands.

Possible deficits in given diameter classes constitute a more difficult situation.

If deficits occur in large diameter classes, the only option may be to wait until smaller trees move into these classes through ongoing growth. Nevertheless, some support treatments are also possible in this case. For example, favoring growth of selected, vigorous individuals by means of appropriate tending measures (based on the principle of positive selection) may significantly speed up this process.

An insufficient number of trees in small diameter classes is another problem. As the case of ESU Browsk 28C clearly demonstrates, over long time periods, advancing from regeneration layer to adult stage is difficult or even impossible for many tree species. Both practical observations and several studies in Białowieża Forest show that two factors are particularly important in this respect.

One factor is low shade tolerance of many local tree species (Brzeziecki and Kienast, 1994; Paluch, 2004, 2005; Brzeziecki et al., 2018a). As pointed out by O'Hara (2014), the relative shade tolerance of trees is often a limiting factor for multiaged silviculture, because it determines the structural arrangement of trees in mixed-species stands. Species with low shade tolerance may be present in the higher canopy layers, but absent below. Thus, mixtures with more shade tolerant species dominating the understory are likely to shift in species composition towards these species (O'Hara et al., 2007; O'Hara, 2014; cf. also Brzeziecki et al., 2020). This is also why, for many tree species, attaining a desirable demographic sustainability status without recurring silvicultural interventions will always be problematical. The stands growing in ESU Browsk 28C illustrate this problem very well. At present, the lower strata in these stands are almost exclusively occupied by hornbeam trees (Fig. 2). Under conditions of Białowieża Forest, hornbeam is the most shade tolerant tree species (Drozdowski et al., 2012; Brzeziecki et al., 2016). For this reason, this species has played most important role in ongoing recruitment processes. Thus, to maintain a mixed character for stands in ESU over the long term, one would need to concentrate in particular on the regeneration phase. For example, creating artificial canopy gaps and exposing mineral soil is indispensable for spontaneous seedling establishment of shade intolerant species with small seeds (birch, aspen, pine). Measures such as direct seeding and/or planting may also appear to be necessary in all cases where natural regeneration, for different reasons, will not succeed (Brzeziecki et al., 2017, 2018b).

Another important problem from the point of view of successful regeneration and recruitment to stand layer concerns browsing by large herbivores. For many decades in Białowieża Forest, numbers of game (especially European bison and red deer) have been very high (Faliński, 1986; Kossak, 1995; Bernadzki et al., 1998; Kuijper et al., 2010; Brzeziecki, 2017; Brzeziecki et al., 2018a). The heavy browsing by ungulates have led to strong species selection, and only those species which survive this pressure (mainly hornbeam) have been able to advance from regeneration to stand layer. Under such circumstances, to enable a development of rich, compositionally diverse regeneration and successful recruitment from regeneration to stand layer, all artificially established or naturally regenerating patches of young growth must be effectively protected (fenced) against large ungulates (Paluch, 2004, 2005; Brzeziecki et al., 2012, 2013, 2018a).

4.3. Question of spatial scale and optimum size of sustainability unit

The degree of correspondence between theoretical equilibrium curves and actual diameter distributions is, to a large extent, a question of spatial scale. In theory at least, the larger the space, the higher the chance that the actual tree distributions will better match the equilibrium models (Rubin et al., 2006; Janowiak et al., 2008; Halpin and Lorimer, 2017). In our case, the size of a basic, sustainable unit of silvicultural planning amounted to about 30 ha. Under conditions of Białowieża Forest such a magnitude seems to represent a reasonable compromise. On the one hand, in case of tree species distinguished by a rather low shade tolerance, it is large enough to enable creating and maintaining a spatio-temporal mosaic of forest patches representing different stand developmental phases (cf. Schütz, 2002). On the other hand, the assumed area of the sustainability unit represents a maximum of what is feasible and manageable from the point of view of forestry practice and detailed silvicultural planning. The defined size of sustainability unit corresponds to the local standard size of forest compartment with clearly defined borders, easily identifiable in the field (Appendix 1). For other forest regions and/or forest types, however, a different size of basic spatial unit, for which an attempt will be done to achieve a long-term goal of population sustainability in mixed forest stands, may appear to be optimal. In case of stands, consisting of shade tolerant species (like silver fir, European beech, Norway spruce, for example), the sustainable stand structures can easily be obtained and maintained at relatively small spatial scales (Pretzsch et al., 2015). In principle, even one hectare may be enough (Schütz, 2001). In case of less tolerant species, significantly larger spatial scales are needed (Schütz and Pommerening, 2013). Also, the local diversity of site and microsite conditions will be important in this respect. Under more homogeneous site conditions, smaller sizes of sustainability units may appear to be possible than under more heterogeneous situations. Nevertheless, the approach adapted and outlined in this paper, is largely scale-independent and it can be applied at different spatial scales. The only (mostly practical) limitation is the minimum scale at which stable demographic structures by means of targeted, purposeful silvicultural operations may be obtained and maintained in the long-term.

4.4. Potential applications (possibilities and limitations)

In 2014, the Białowieża Forest as a whole (both the Polish and Belarussian part) received a status of World Heritage Site and extensive areas of it were subject to strict protection (Brzeziecki et al., 2018c). Thus, demographic approach can only be applied in that Białowieża stands in which, according to current legal regulations, human activities are still permissible. The practical application of the demographic equilibrium approach is, however, by no means limited to Białowieża Forest. A potentially important advantage of demographic approach is its relative simplicity. Nevertheless, to accomplish this approach in practice, some basic requirements have to be fulfilled (Fig. 8). Maybe the most important one concerns the construction of species-specific growth and mortality functions which jointly determine shapes of equilibrium diameter distributions of relevant tree species. To obtain the quantitative parameters of these functions, data from at least two successive forest inventories are needed. At the initial stage, when the appropriate data are missing, also more general growth and mortality functions, parameterized by means of data collected in similar/adjacent forest objects, can be used, as a kind of first approximation. For example, the National Forest Inventory data, representing proper stand structures, could be of a great help here. Another requirement concerns delimitation of areas (forest compartments) playing the role of basic forest sustainability and regulation units. For every sustainability unit, one needs also to determine the optimal level of an overall stand basal area and the desirable tree species composition. This can be done more or less arbitrarily; however, the general goal would be creating and maintaining as diverse (in terms of tree species composition) stands as possible, under constraints imposed by a given set of environmental conditions. Forest inventories (using permanent sample plots), executed within each sustainability unit, would provide data which are needed to calculate basic stand parameters (including the value of periodic stand volume increment) and to determine the actual, species-specific diameter distributions. These distributions can be further compared with looked-for, target models. Resulting differences would form a basis for silvicultural decisions and actions aimed, generally, at bringing gradually existing tree population structures closer to the desirable, sustainable state. The results of the repeated inventories could also be used to check, to which

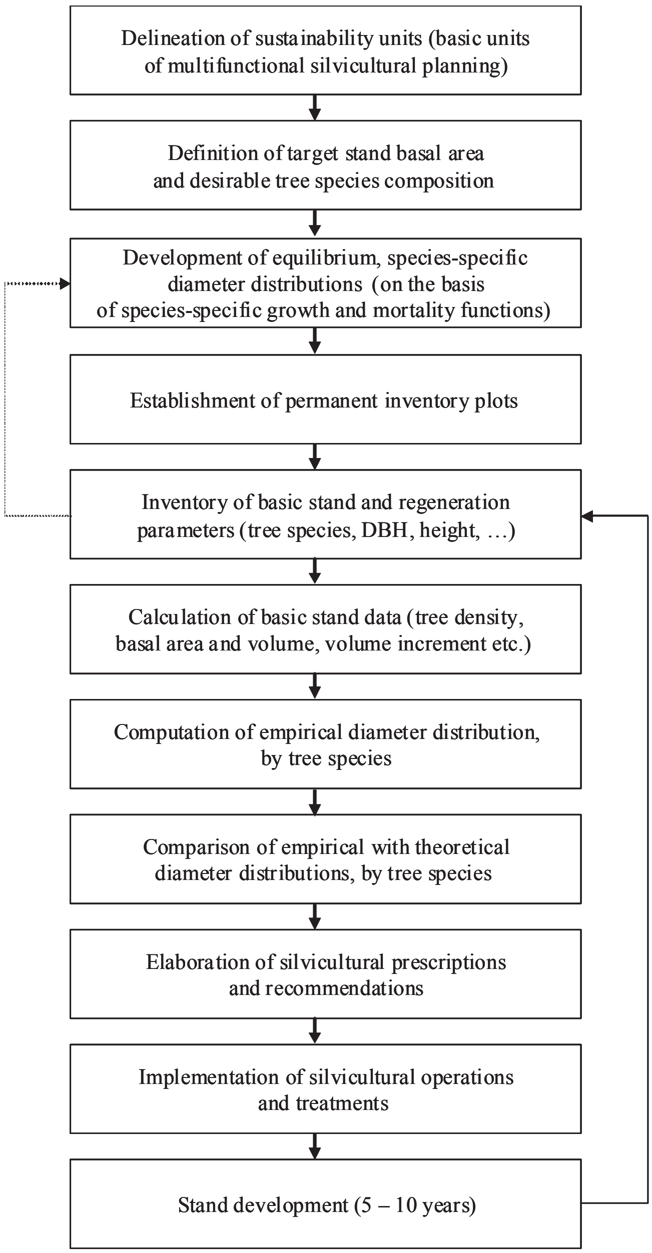

Fig. 8. A flow chart presenting most important steps for applying the demographic equilibrium approach as a structure and stocking regulation tool in mixed-species and multiaged forest stands.

extent this overall goal is achieved. Several stand variables and parameters may be used in this respect: stand volume increment, actual numbers of recruits (in comparison to model values) and discrepancy coefficients measuring a degree of similarity between theoretical and empirical species-specific diameter distributions.

In comparison to other, more conventional regulation approaches based on diameter distributions (like the BDq method – cf. O'Hara and Gersonde 2004), a big advantage of demographic approach is that it allows to take into account the differences in basic life-history traits (such as growth and mortality patterns) between particular tree species building mixed stands. Thanks to this, the demographic approach can be applied for stands consisting of any given number of tree species. What is more, in contrast to BDq method, in case of demographic approach one does not need to define explicitly a target tree diameter. This allows for development of stands containing large and very large trees, which are often considered to be important components of multifunctional forest stands (Bauhus et al., 2009; Grzywacz et al., 2018). The important feature of the demographic approach is also that it is spatially independent. It means that it can be used both at the level of a single sustainability unit, as well as at a broader spatial scale, by incorporating several independent, basic planning units and performing appropriate calculations for aggregated forest areas.

The demographic approach to stocking regulation is less stringent than other existing, comparable methods. It does not focus so much on volume increment, yield, financial income and other similar features which traditionally have been considered to be important in forestry. In case of demographic approach, these parameters play some role, as well, however, the main focus is on preserving of a mixed character of forest and on maintaining a population sustainability of constituent tree species, within the spatial limits of the defined, basic sustainability units.

5. Conclusions

Nowadays, maintaining diverse species mixtures and balanced tree demographic structures is very much indicated and needed, as a basic prerequisite if high levels of forest biodiversity and other important ecosystem services are to be retained (O'Hara, 2014, 2016; Halpin and Lorimer, 2017). Moreover, creating mixed-species and multiaged/multisized stands may be the best strategy assuring high adaptation potential of forests to ongoing and anticipated environmental change (Brang et al., 2014; O'Hara, 2014; Ammer, 2019). On the basis of the results obtained for an exemplary, basic forest sustainability unit we suggest that achieving these important tasks and challenges of contemporary silviculture can be greatly facilitated by application of the demographic equilibrium approach towards growing stock regulation in mixed-species stands.

Authors' contributions

B.B. conceived the ideas and designed methodology; B.B., S.D., K.B., M.C., W.B. and L.G. collected the data; B.B., K.B., M.C., S.D. and J.Z. analyzed the data; B.B. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118694.

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