Forest Ecology and Management 461 (2020) 117964

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Plantation forests cannot support the richness of forest specialist plants in the forest-steppe zone

Tamás Rédei*, Anikó Csecserits, Barbara Lhotsky, Sándor Barabás, György Kröel-Dulay, Gábor Ónodi, Zoltán Botta-Dukát

Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány u. 2-4., Vácrátót 2163, Hungary
GINOP Sustainable Ecosystems Group, Centre for Ecological Research, Klebelsberg Kuno u. 3., Tihany 8237, Hungary

ARTICLE INFO

Keywords:
Forest management
Land use history
Mechanical site preparation
Pedunculate oak
Black locust
Alien species

ABSTRACT

In forestry, several types of management practices are used, which have significant effects on species richness and composition. A number of studies concerning the effect of management on biodiversity have been conducted in the tropical and temperate forest zones. This topic is less studied in the forest steppe biome, where the reestablishment of plants from the surrounding patches is more limited than in the forest biome. Most studies compare alien plantations with seminatural forests. However, the effects of dominant tree species is mixed with the effect of the site preparation and site history in such comparisons, due to intensive site preparation in case of forest plantations.

In this study, we separate the effect of these management elements. We examined the potential of currently used forestry protocol in preserving the plant biodiversity of the forest herb layer in the Pannonian sand forest steppe using 266 forest plots from the Kiskunság sand region in Hungary. The total richness and richness of habitat preference groups (forest specialists, grassland specialists, native weeds, and aliens) were compared in natural and plantation forests of different tree species to explore the effects of dominant tree species and site preparation on the species composition. Factors determining the richness of forest specialists in plantations were analyzed by fitting a regression tree, and the habitat preference of these species was described by their fidelity to the forest types.

Our results show that total species richness is less sensitive to management than the richness of some species groups with a specific habitat preference. Forest specialist species can survive almost only in continuous seminatural oak forests, that is, in forests that are continuously present and do not undergo any site preparation. They are completely missing from young plantations, most likely because site preparation completely removes them. Their limited recolonization is possible only in plantations of native trees in landscapes where seminatural oak forests have been continuously present. Even under these conditions, only half of the forest specialist species are able to recolonize in the plantations. Grassland specialists, on the other hand, are present in every forest type but with low richness. Site preparation acts as a colonization window for weeds and aliens. However, while the richness of weeds is the highest in young plantations and decreases in established plantations, probably due to the canopy closing, the richness of aliens is the same in both young and established plantations.

Considering our results, the current forestry protocol is hardly suitable for maintaining the plant biodiversity of forests in the forest steppe zone, therefore, management practices should be changed to focus more on the conservation of these endangered habitats.

Nomenclature: Király (2009).

1. Introduction

It is well known that the type and intensity of and changes in present and historical land use are major determinants of biodiversity in most ecosystems (Harding et al., 1999; Foley et al., 2005; Newbold et al., 2015). In forests, several types of management practices are employed to enhance cost effectiveness and maximize timber production, such as clear-cutting, tree plantation, selective thinning, and shrub clearing, which have significant effects on the actual and future species richness and composition of forests (Hansen et al., 1991; Paillet et al.,

* Corresponding author.
E-mail address: redei.tamas@okologia.mta.hu (T. Rédei).

https://doi.org/10.1016/j.foreco.2020.117964
Received 13 December 2019; Received in revised form 29 January 2020; Accepted 31 January 2020
Available online 12 February 2020

2010). Clear-cutting and tree plantation are the management practices that have the greatest impact on biodiversity. They interrupt the continuity of forest cover or create new forest patches. The soil and the species composition preserve the effects of a deforested period for a long time (Peterken and Game, 1984; Foster, 1992; Hermy, 1994; Koerner et al., 1997, 1999), even on a millennial time scale (Dupouey et al., 2002).

Plantation forests are widespread worldwide (Paquette and Messier, 2010). Planted on former agricultural lands or mining areas, they are often used to restore plant cover (Vítková et al., 2020), but the biodiversity of the resulting stands depends on the original land use and on the planted tree species (Stephens and Wagner, 2007; Bremer and Farley, 2010). Fast growing alien tree species are often used (Richardson, 2001). These plantations of alien trees are usually effective for timber production but inefficient for regenerating the original biodiversity (Paquette and Messier, 2010; Newmaster et al., 2011).

Although total plant species richness in plantations is seldom lower than in natural forests, their species composition differs: Species with wide habitat preference (generalists) and species of repeatedly disturbed habitats (weeds) substitute the forest specialists of the original species pool (Michelsen et al., 1996). Moreover, plantations (especially those of alien trees) are often hotspots of alien plant species in the landscape (Csecserits et al., 2016; Medvecká et al., 2018). Therefore, from the viewpoint of nature conservation, alien tree plantations are less favorable than the native ones (Magura et al., 2000; Dickie et al., 2014; Brundu and Richardson, 2016; Bazalová et al., 2018; Šibíková et al., 2019).

Most of the previous studies have compared seminatural forests (i.e. spontaneously developed stands of native trees) with alien tree plantations (Michelsen et al., 1996; Bazalová et al., 2018; Šibíková et al., 2019). Seminatural and plantation forests of the same dominant native tree were rarely compared; however, it is necessary to separate the effect of the dominant tree species from the effect of the management practices. This separation would be particularly important in areas where the natural renewal of trees is limited due to unfavorable environmental conditions (e.g. forest steppe zone); thus, the proportion of the natural forests decreases, and these forests are often replaced by plantations of native or alien tree species.

The transitional woodland–grassland vegetation of forest steppe zones covers large areas worldwide (Berg, 1958; Leach and Givnish, 1999; Kitzberger, 2012; Erdős et al., 2018a). Since their mosaic characteristics, resembling remnants of forest steppe habitats, harbor a high diversity of plant species, their conservation value can be significant (Chytry et al., 2012; Hais et al., 2016; Bátori et al., 2017). The Pannonian forest steppe is one of the westernmost enclaves of the Eurasian forest steppe zone. It is located in the southeastern part of Central Europe and consisting of a mosaic of dry forests and steppe vegetation (Zólyomi, 1957; Zólyomi and Fekete, 1994; Molnár, 2003; Erdős et al., 2018a, 2019).

Although the seminatural forests of the Pannonian sand forest steppe region (dominated by oak or white poplar) are critically endangered (Borhidi and Sánta, 1999), and their area is decreasing radically (Biró et al., 2018), they still have a high importance in maintaining the biodiversity of the landscape (Erdős et al., 2018b). These seminatural forests were probably managed as coppice and grazing forests in the past centuries, but, according to the maps, the forest cover was permanent here (Biró, 2008). All other forests of this region are intensively managed by clear-felling and often by replacing the native tree stands with alien tree plantations (mainly black locust, hybrid poplars, and black or Scots pine) using heavy equipment for site preparation. The effects of this management protocol on the biodiversity of this zone's forests are rarely described.

In this study, we compared the plant species richness and composition of the understory layer in plantation and seminatural forests of the Pannonian sand forest steppe region. We separated the effect of the dominant tree and the effect of the management type (spontaneous regeneration or planting after mechanical site preparation). Because total species richness alone is often ineligible for detecting the biodiversity differences between natural and plantation forests (Michelsen et al., 1996; Battles et al., 2001; Wulf, 2004), we also compared the richness of plant species groups with different habitat preferences or origins. Since the survival of forest specialist plants in the region depends on the presence of forest habitats, we paid special attention to this species group.

Our questions were the following:

1. Is there a difference in the total plant species richness, in the richness of plant species groups with different habitat preferences (forest specialists, grassland specialists, weeds) and origins (natives and aliens), and between young and established plantation forests and seminatural forests?
2. Does the species identity of the dominant tree affect the size of the species richness difference between the established native plantation forests and the seminatural forests?
3. Is there a difference in plant species richness among established plantations of different tree species?
4. Which factors (tree species, environmental conditions, landscape context) determine the species number of forest specialist species in established plantation forests?
5. Which forest types (categorized by management type and dominant tree) are preferred by forest specialists?

2. Materials and methods

2.1. Study area

Our study area, the Kiskunság, is an inland sand dune landscape in the center of the Carpathian Basin between the Danube and Tisza rivers in Hungary, with a total area of 7500 km^2. The climate of the region is continental with a sub-Mediterranean influence. The mean annual temperature is 10.4 °C with monthly means ranging from −1.9 °C in January to 21.1 °C in July. Mean annual precipitation is 500–550 mm, with a peak in June, and a second, minor peak in November, with a gradual decrease from North to South and from West to East (Kovács-Láng et al., 2000). The dominant substrate is calcareous sand, on which various sand soil types with high sand (over 90%) and low humus content (below 3%) have developed (AGROTOPO, 1994). The elevation is between 110 and 160 m a.s.l. in the entire region.

The natural vegetation of the region was a mosaic consisting of sand forest steppes with wetlands in lower elevation areas (Zólyomi, 1989). The major components of the forest steppe complex, the oak and poplar forests and dry sand grasslands, continuously persisted during the Holocene with a significant extent (Fekete et al., 2010; Magyari et al., 2010). The area of the seminatural forests has been reduced heavily in the last centuries (Biró, 2008). Nowadays, the area covered by seminatural oak forests (mainly *Quercus robur* dominated stands, sometimes mixed with *Q. pubescens* and *Q. cerris*) and closed seminatural poplar stands (dominated mainly by *Populus alba, P.* × *canescens* and rarely *P. nigra*) amounts to 1750 ha (Biró, 2008). In the past centuries these seminatural forests were coppiced to gain firewood and/or grazed by cattle. The traditional land use supported the persistence of biodiversity (Košulič et al., 2016; Roleček et al., 2017). According to the military mappings of the region in the last 250 years, oak stands have not colonized new areas, while the native poplar established several new stands in the previously unforested landscape. Due to the synergy of the dry climate and the low water retention capacity of the sand soil, this region is close to the lower timberline (Mátyás et al., 2018); therefore, the regional species pool is strongly impoverished concerning forest specialists (Fekete et al., 2010).

Since the end of the 18th century forest cover has grown due to the afforestation activities of the 19th and 20th centuries. Several alien trees have been introduced: Black locust (*Robinia pseudo-acacia)* was planted from the end of the 18th century, black and Scotch pine (*Pinus nigra and P. sylvestris)* from the end of the 19th century, and the exotic hybrid poplar (*Populus* × *euramericana)* from the middle of the 20th century. In 2018, in Bács-Kiskun county (which covers nearly the entire study region), 58% of the 186 000 ha of forests consisted of alien tree plantations: 60 000 ha black locust, 44 000 ha pine, and 4 000 ha exotic poplar dominated stands (estimation is based on the forest management plans of the region, considering personal interviews with the management of the local forestry).

Forests are being felled in the region at a relatively young age: locust tree at 25–30 years, pine at 30–40 years, native poplars at 30–50 years, exotic poplar at 20–25 years, and pedunculate oak at 80–90 years (based on the data of the local forestry). In the recent few decades the regeneration of the oak stands has become more difficult due to the lowering of the ground water table. To reach the mandatory canopy cover (60%) in the plantations in a relatively short time, the current forestry practice in the region follows the procedure outlined below: clear felling, stump removal, mechanical site preparation with heavy equipment (deep ploughing, manipulating the soil structure and microtopography, and removing the topsoil containing the roots and propagules of the herbs and shrubs), planting of tree saplings, and mechanical weed control during establishment. Stump removal and mechanical site preparation are often employed in the case of planting oak, pine, and exotic poplar. From the viewpoint of the vegetation, this standard procedure results in an agricultural field-like area. Native poplar and black locust are often coppiced, but in this study, we sampled stands that were planted using the aforementioned procedure (*henceforth* we use the term *plantation forest*). Sometimes, in the first few years after planting, crops (e.g. maize, pumpkin, or melon) are planted between the lines of the saplings. These techniques result in barren young plantations where the recolonization of the plant species from the surrounding landscape can start just after the 2–10 years of intensive management (Fig. 1).

Fig. 1. In a young black pine plantation the alien weed *Chenopodium aristatum* is one of the first colonizers following the site preparation on sand, in Kiskunság, Hungary.

2.2. Field sampling

The field sampling was done within the field site network of the Kiskun LTER program in June–August of 2006–2008 (Csecserits et al., 2011; Rédei et al., 2008; 2014). This network consists of sixteen 6 km × 6 km sites representing the originally forest steppe dominated subregions of the Kiskunság (Fig. 2), covering all major land cover types. For details on sampling design see Rédei et al. (2008). In each 36 km^2 site three independent patches (or less, if there were not three available independent stands) were sampled by recording the species lists and the visually estimated percentage cover of the vascular plant species in one 20 m × 20 m plot in the dominant habitat types. In this study, data on only the following habitat types was considered: seminatural forests (with mixed age structure), established plantation forests (close to the age of final felling), and young plantations (less than 5 years after site preparation and planting trees).

Altogether 266 plots were included in the analyses. A total of 110 plots were made in established alien tree plantations (44 in black locust, 47 in black and Scots pine, and 19 in exotic poplar stands); 56 plots in established native tree plantations (39 in native poplar and 17 in oak stands); 42 plots in young plantations; and 37 plots in seminatural forests. The age of the sampled plantations was close to the regional maximum. In the case of the young plantation plots, we did not consider the species identity of the planted tree, since, due to its low biomass and cover, its effect is probably negligible compared with that of the site preparation. The 37 seminatural forest plots had at least 60% closed canopy layers and consisted of 28 poplar and 9 oak dominated plots. The sampled seminatural poplar forests were spontaneous old stands. The nine sampled natural oak forests were old stands with continuous forest cover since 1780, according to the available sources (first, second, and third military mapping of the Habsburg Empire), and mainly with mixed age. In order to better represent this habitat type, we made 21 additional plots between 2010 and 2018 in seminatural oak forests in the Kiskunság region, with the same habitat history, but outside the Kiskun LTER site network (Fig. 2).

2.3. Local environment and potential landscape level drivers of diversity of forest plantations

The local environment was characterized by two climatic variables (annual precipitation and mean annual temperature) and soil data. Annual precipitation was derived from interpolated climatic data from 1961 to 1990 collected by the Hungarian Meteorological Service (HMS, 2001), whereas temperature data came from the WorldClim database (Hijmans et al., 2005). Soil properties, including chemical reaction (pH) and carbonate status, organic material content (ton/ha), percentage productivity value, and genetic soil type, were obtained as categorical variables from the AGROTOPO database (1994). For soil data, see details in Csecserits et al. (2016).

Landscape variables were derived from the habitat maps of the 16 study sites of the Kiskun LTER on the basis of aerial photographs taken in 2005 (Rédei et al., 2008). The landscape context of the plots was characterized by the current total percentage cover of natural forest steppe habitats (including seminatural dry and semidry grasslands, shrublands, and natural forests) and by the current percentage cover of seminatural forests in the buffer zone with a 500 m radius around the plots. GIS related work was done using ArcGIS 9.2 software (ESRI, 2006).

Historical continuity of the natural oak forest stands was determined using a series of habitat maps of the sites based on the first (1780) and second (1830) military mapping of the Habsburg Empire, archive aerial photographs from the 1950 s and 1980 s, and the actual habitat maps (based on the aerial photographs from 2005). Forest cover of the landscape was regarded as continuous if these forests were present in the 6 km × 6 km landscape section (i.e. the study sites of Kiskun

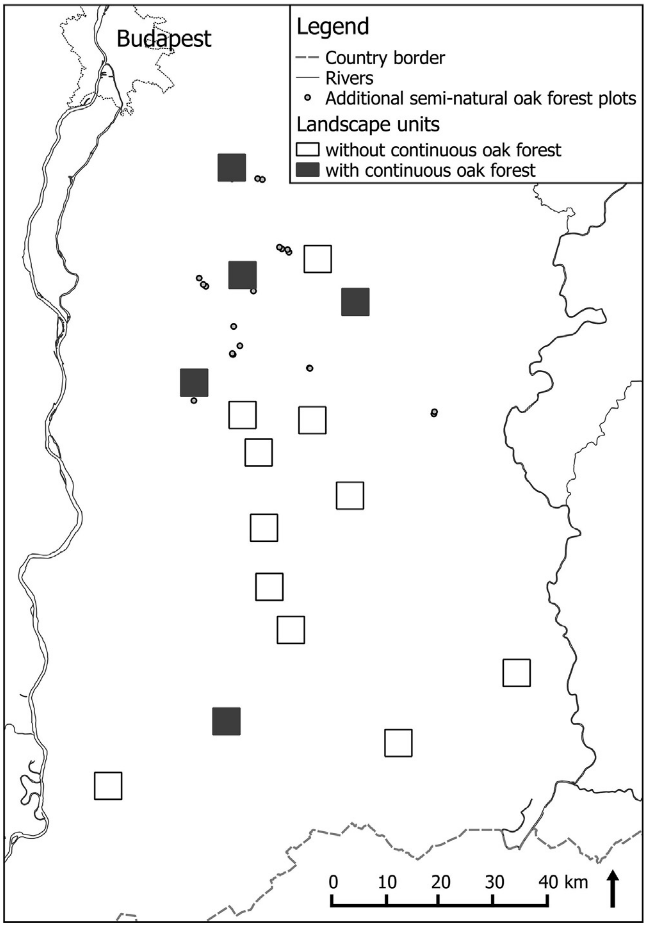

Fig. 2. Map of the study area with the 16 sampling sites (gray: with continuous oak forests, white: without continuous oak forests) and additional plots placed in seminatural oak forests (circles).

LTER) in all of the documented periods and discontinuous when they were missing in at least one period on the basis of the evaluation of these maps.

2.4. Data analysis

To analyze the effects of the dominant tree species and management type on plant species with different habitat preference, we categorized these species on the basis of their phytosociological behavior (Borhidi, 1995). We used the following categories: forest specialist, that is, herbaceous plants of mesophilous and dry deciduous forests (*Querco-Fagetea* and *Quercetea pubescenti-petreae*); grassland specialists, that is, plants of dry grasslands (*Festuco-Brometea*) and mesic or wet meadows (*Molinio-Arhenatheretea);* weeds, that is, native or archeophyte plants of ruderal habitats or arable fields, requiring continuous disturbance; aliens, that is, spontaneously occurring plants nonnative to the Kiskunság region introduced after the 15th century. Spontaneous occurrences of species cultivated by forestry (*Pinus nigra, Pinus sylvestris, Populus* × *euramericana*) or agriculture (*Persica vulgaris, Juglans regia, Triticum aestivum* etc.) are regarded as aliens. The categorization of the species is published in the Mendeley Data. Since composition of the tree and shrub layer is strongly controlled by the forest management techniques (plantation, shrub clearing, and selective thinning), only species of the herb layer were used in the analysis (Schmidt, 2005; Standovár et al., 2006); thus, in the plantations, the planted trees were excluded, even if they were only saplings.

Total species richness and richness of the defined species groups were compared first among the three main forest types (seminatural forests, young forest plantations, and established forest plantations). Then within established forest plantations, five types differing in the planted tree species were compared. In both cases, generalized linear models were fitted, using negative binomial distribution and log link function (Venables and Ripley, 2002). Pairwise comparisons were done using the Tukey post-hoc test to avoid inflation of Type I error.

For evaluating how the dominant trees species identity influences the difference in species richness between seminatural and plantation forests of the same tree, a subset of plots dominated by oak or native poplar was studied, because only these two tree species occur both in seminatural and plantation forests. We fitted a generalized linear model with two categorical independent variables – forest type (seminatural or plantation forest) and dominant tree species (oak or native poplar) – to species richness data in this subset and tested the interaction between these independent variables. Significant interaction means that species identity has an effect on the difference between seminatural and plantation forests.

To explore the relationship between the richness of forest specialists and the predictor variables (environmental factors, landscape context, and planted tree species) in plantations, conditional inference-based decision trees were fitted. Decision trees, also known as classification and regression trees (Breiman et al., 1984), are nonparametric statistical methods that can handle nonlinear relationships and very large sets of mixed type (i.e. both categorical and continuous) predictors. The results are easy to interpret and indicate the variable that most significantly discriminates between classes (Crawley, 2007). Furthermore, as decision trees handle the predictors one by one, they are essentially free from problems caused by multicollinearity. The selected algorithm offers unbiased variable selection and a statistically sound stopping rule (Hothorn et al., 2006), which eliminates the variable selection bias and problems of under- and overfitting.

For exploring the habitat preference of forest specialist species, indicator species analysis (Dufrene and Legendre, 1997) was done with eight groups of plots (i.e. all existing combinations of management type and tree species), allowing the combination of these groups as suggested by De Cáceres et al. (2010).

All statistical analyses were done in R 3.5.0 environment (R Core Team, 2018), using MASS (Venables and Ripley, 2002), multcomp (Hothorn et al., 2008), party (Hothorn et al., 2006), and indicspecies (De Cáceres and Legendre, 2009) packages.

3. Results

We found altogether 430 vascular plant species in the 266 plots, including 34 herbaceous forest specialists, 163 grassland specialists, 63 native weeds, 77 herbaceous generalists (i.e. species without clear habitat preference), and 39 native woody species. We found altogether 54 aliens in the flora.

Total species richness was significantly higher in seminatural forests than in either old or young plantation forests, which do not differ from each other significantly (Fig. 3a). Richness of forest specialist species significantly differed between any pair of these three main types: It was highest in seminatural forests and lowest in young plantation forests (Fig. 3b). Number of grassland specialists did not differ among the three groups (Fig. 3c). Number of weeds was significantly higher in young plantations and significantly lower in seminatural forests than in the other two habitat types (Fig. 3d). Number of aliens was significantly lower in seminatural than in plantation forests, but it did not differ between young and old plantation forests (Fig. 3e).

We found a significant interaction between management type (seminatural vs. plantation) and dominant tree (oak vs. native poplar) only in the number of forest specialist species: The difference between seminatural and plantation forests was significantly higher if the dominant tree was oak. Looking at the total species richness and richness of the other studied species groups, we can conclude that the identity of the dominant tree had no significant influence on the

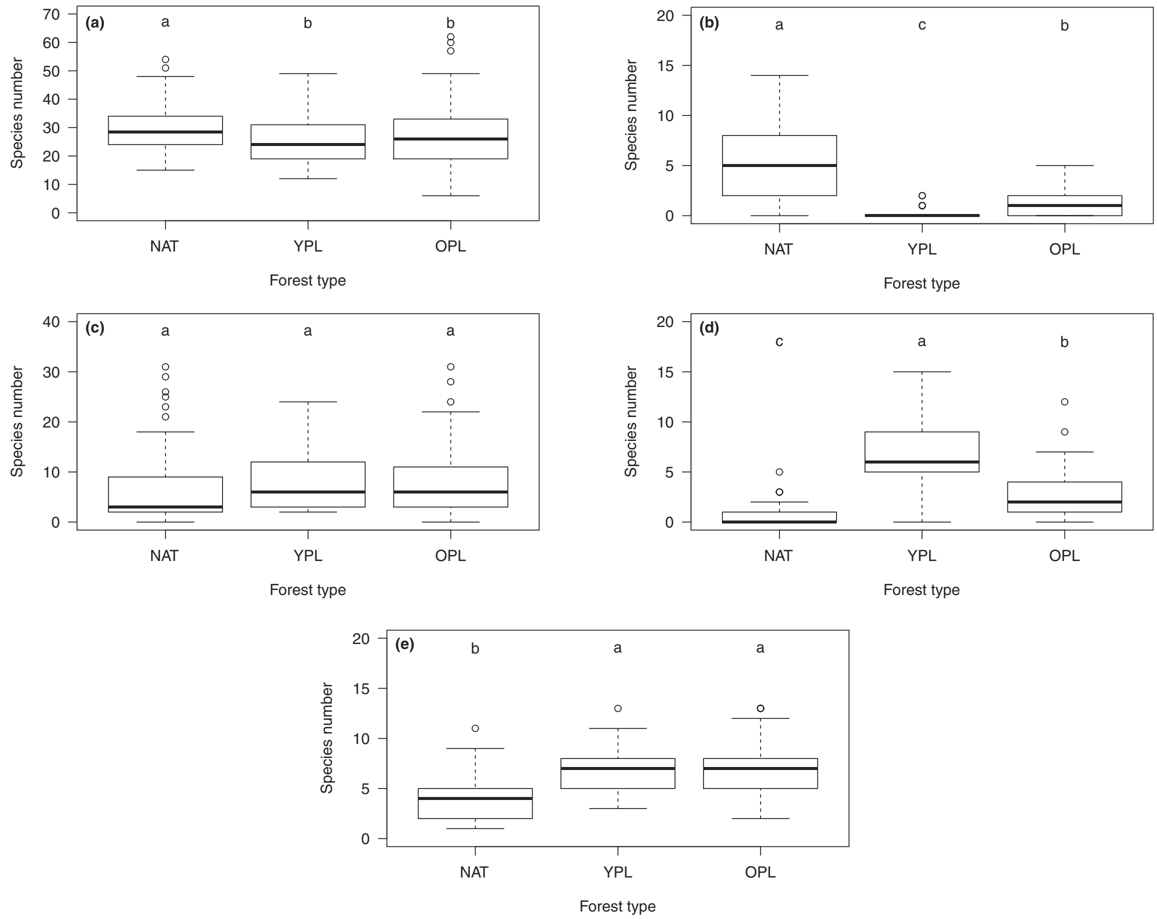

Fig. 3. Species richness of the herb layer in the three main forest types. NAT: seminatural forests, YPL: young plantation forests, OPL: old plantation forests. Subplots are the followings: (a) all species; (b) forest specialists; (c) grassland specialists; (d) weeds; (e) aliens. Different letters indicate significant differences among the three main management type. Note that scaling of y-axis varies among subplots for a better visibility of differences between management types.

Table 1
Results of the generalized linear model fitted with two categorical independent variables – forest type (seminatural or plantation forest) and dominant tree species (oak or native poplar) – to species richness data, and testing the interaction between independent variables. Positive z-value means that the oak stands are richer than poplar ones (Oak vs Native Poplar) and the seminatural forests are richer than plantations (Seminatural vs Plantation). The difference between natural and plantation forest is higher if the dominant tree is oak (Interaction).

	Oak vs Native Poplar[1]		Seminatural vs Plantation[2]		Interaction[3]	
	z-value	P-value	z-value	P-value	z-value	P-value
All species	−0.067	1.000	1.051	0.635	0.478	0.947
Forest	**7.593**	**< 0.0001**	**6.017**	**< 0.0001**	**2.691**	**0.0208**
Grassland	**−4.258**	**< 0.0001**	1.066	0.622	−0.975	0.686
Alien	−2.350	0.0547	**−6.158**	**< 0.0001**	−2.009	0.1260
Weed	−1.660	0.2534	**−6.673**	**< 0.0001**	−2.254	0.0688

difference between seminatural and plantation forests. Richness of grassland specialists was significantly higher in poplar stands, but management type had no significant effect on the richness of this group. On the other hand, the dominant tree had no significant effect on the richness of weeds and alien species, while management type had: The richness of these two species group was significantly higher in forest plantations (Table1).

Comparing the established plantation forests dominated by different tree species, we found that the total species richness in the herb layer was lower in black locust plantations than in the plantations of the other trees, excluding pine (Fig. 4a). Richness of forest specialist species was significantly higher in oak plantations than in the other plantations. Native poplar, pine, and black locust plantations did not differ from each other in this respect, while alien poplar plantations varied significantly: Forest species were almost completely absent here (Fig. 4b). The number of grassland specialists was lowest in black locust and oak plantations and highest in alien poplar plantations (Fig. 4c). Native poplar and pine plantations had intermediate values; they did not differ from either oak or alien poplar stands. Species identity of the dominant tree had no significant effect on richness of native weed and alien species in the plantations (Fig. 4d, e).

The regression tree fitted on species richness of forest specialists in the established plantations explained 32.66% of the total variance, and the dominant tree proved to be the most important predictor (Fig. 5). In the first split, oak plantations were separated from the rest because of their higher richness in forest specialists (median 3). The second group (i.e. plantation dominated by other species, not oak) was further divided on the basis of the historical continuity of the seminatural oak

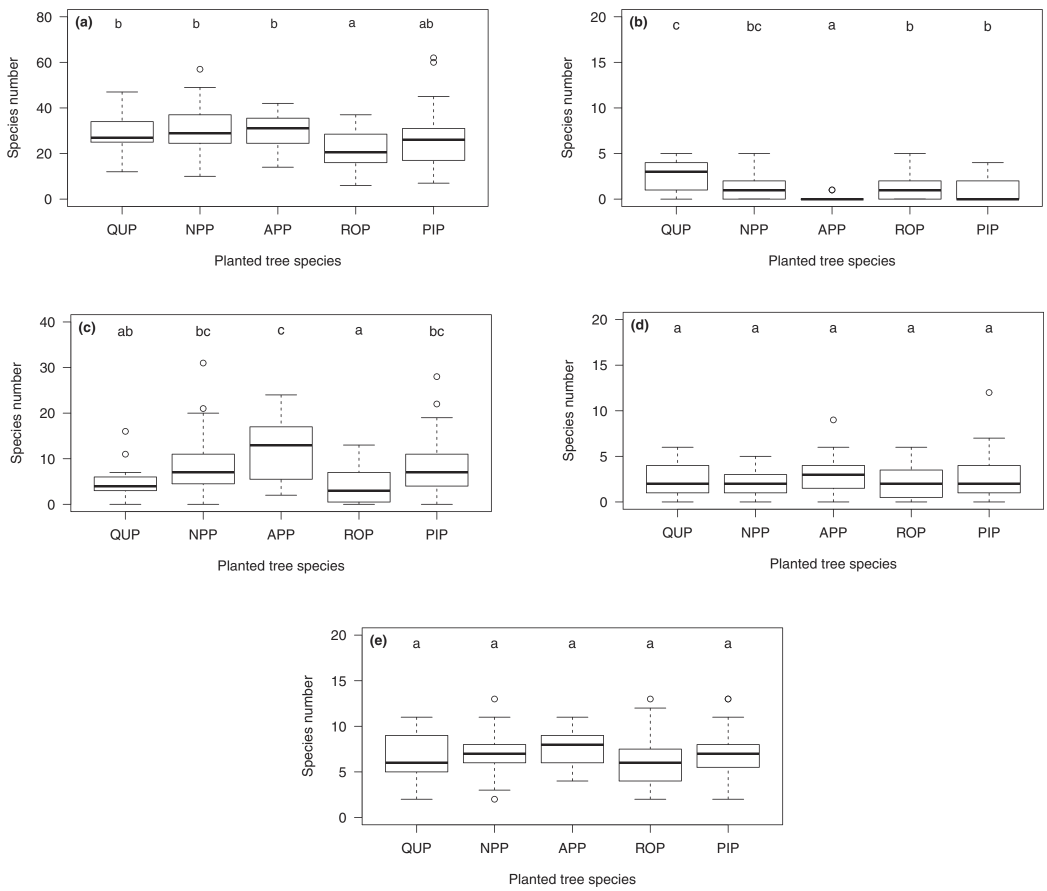

Fig. 4. Species richness of herb layer in the five old plantation forest types. QUP: oak plantation, NPP: native poplar plantation, APP: alien poplar plantation, ROP: black locust plantation, PIP: pine plantation. Subplots are the followings: (a) all species; (b) forest specialists; (c) grassland specialists; (d) weeds; (e) aliens. Different letters indicate significant differences among the five plantation forests. Note that scaling of y-axis varies among subplots for a better visibility of differences between dominant trees.

forests in the surrounding area in the last 230 years. If the presence of seminatural oak forests in the landscape was continuous, the species richness was significantly higher (median 2). Within sites where seminatural oak forests were not continuously present in the surrounding landscape, average yearly precipitation was the most important predictor. Below 540 mm yearly precipitation, the species number of forest specialists was significantly lower (median 0) than above this value (median 3).

Out of 34 forest specialist species, 20 had a significant habitat preference; 14 of them preferred seminatural oak forests, while three other species preferred oak forests irrespective of their natural or plantation origin, one species preferred seminatural forests irrespective of the dominant tree, and another species preferred stands dominated by native trees (both natural and plantation forests). The alien tree stands did not have their own indicator species within this group; however, one species preferred oak and black locust, one species oak and pine forests, and finally one preferred all established stands but alien poplar. All of the 12 species having no significant preference were infrequent in the dataset. Eight of them occurred in natural oak forests only, while the occurrences of the remaining four species were distributed in natural and plantation forests with native tree species (Table2). The habitat preference data of the whole species pool is

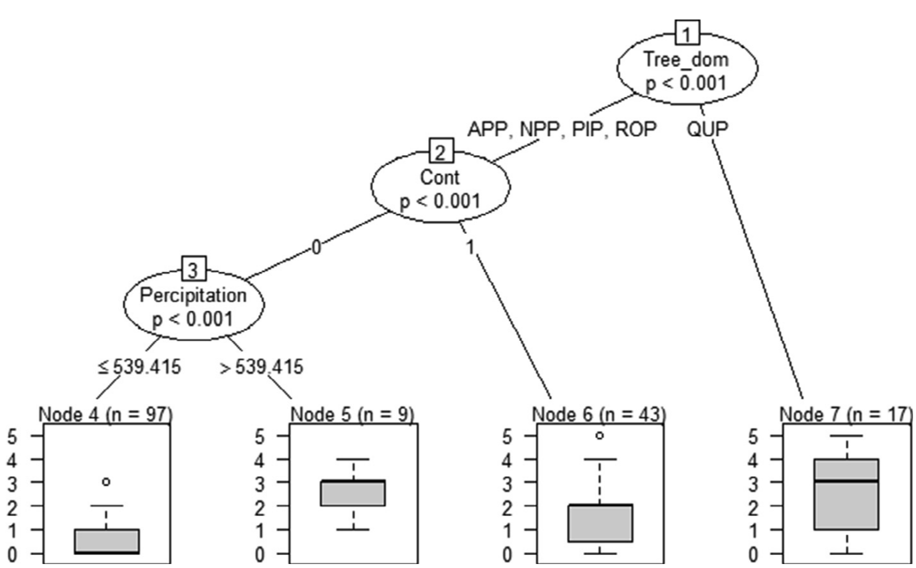

Fig. 5. Regression tree model of the richness of forest specialist species in the sampling plots. Each node is described by the splitting variable used at the split, the Bonferroni-corrected significance (P-value) of the split and the values at which the split occurs. At each terminal node the number of observations (n) is given along with boxplots of the richness of forest specialists. Abbreviations in the circles (nodes): Tree—main tree species, Conti—continuity of oak forests in the sampling sites, pscpyy—mean annual precipitation. For habitat codes see Fig. 4.

Table 2
Results of the indicator species analysis. Frequency: Number of occurrences of the species. Habitats codes show the preferences of the forest specialists. QUN: seminatural oak forests, NPN: seminatural poplar forests, QUP: oak plantations, NPP: native poplar plantations, ROP: black locust plantations, PIP: pine plantations. Habitat codes in brackets show that the species was present in that habitat, but the test was not significant because of its rarity.

Species	Frequency	Habitat
Brachypodium sylvaticum	65	QUN + QUP
Geum urbanum	61	QUN + QUP + ROP
Viola hirta	57	ROP + PIP + NPP + QUP + NPN + QUN
Polygonatum latifolium	40	QUN
Polygonatum odoratum	36	NPN + QUP
Lithospermum officinale	33	QUN + QUP + NPN + NPP
Clinopodium vulgare	31	QUN + QUP
Poa nemoralis	17	QUN + QUP
Convallaria majalis	17	QUN
Cucubalus baccifer	15	QUN + QUP
Elymus caninus	15	QUN
Mycelis muralis	11	QUN + QUP + PIP
Astragalus glycyphyllos	9	QUN
Galeopsis pubescens	7	QUN
Silene nutans	7	(QUN + NPN + NPP)
Veronica chamaedrys	5	(QUN + QUP + NPP)
Lapsana communis	4	QUN
Lithospermum purpureocoeruleum	4	QUN
Viola reichenbachiana	4	QUN
Carex spicata	3	QUN
Carex sylvatica	3	QUN
Melica altissima	3	QUN
Festuca heterophylla	2	(QUN)
Ficaria verna	2	(QUN + NPN)
Moehringia trinervia	2	QUN
Scrophularia nodosa	2	QUN
Arum orientale	1	(QUN)
Bromus ramosus	1	(QUN)
Circea lutetiana	1	(QUP)
Galium odoratum	1	(QUN)
Melampyrum nemorosum	1	(QUN)
Pulmonaria mollissima	1	(QUN)
Salvia glutinosa	1	(QUN)
Stachys sylvatica	1	(QUN)

attached in the Mendeley Data.

4. Discussion

4.1. Differences in species richness between seminatural forests and plantations

We found significant differences among the three studied management types concerning the herb layer: The seminatural forests had the most forest specialist species, while young plantations the most weeds. Both the young and old established plantation forests had more alien species compared with the seminatural forests.

In accordance with previous studies (Michelsen et al., 1996; Battles et al., 2001; Wulf, 2004; Durak et al., 2015), total species richness was less sensitive to the management type of the stands than richness of species groups with a defined habitat preference. Since the landscape is relatively rich in disturbance tolerant generalists and disturbance requiring weeds, they can colonize and establish themselves in the plantations, thus partially balancing the decrease of species richness due to the disappearing of specialists.

Although the role of management type proved to be the most important factor in maintaining biodiversity, dominant tree species also played an important role. We found significant differences concerning the herb layer among the plantation forests dominated by different tree species. The oak plantations harbor the highest number of forest specialist species. These species have adapted to the environmental conditions provided by the oak forests. Oaks are often planted on the best quality sites and this, paired with the relatively long cutting interval, facilitates temporal recolonization for some well-spreading specialists. However, their richness in plantations is far below the richness of seminatural stands.

Black locust plantations proved to be the less favorable environment for plant biodiversity (less total species richness in the herb layer), probably because the shorter cutting interval and the local environment of its ground floor (high soil nitrogen content, special light conditions caused by late leafing date in spring and heavily closed canopy in summer) hamper the presence of several species (Campagnaro et al., 2018; Vítková et al., 2017).

Comparing the stands of the two native tree species, the difference in the richness of forest specialists between seminatural and plantation forests is higher if the dominant species is oak. This is due to that fact that the richness of this group is significantly higher in the seminatural oak stands as in the seminatural poplar stands. This difference is more or less removed by the procedures of the tree plantation, resulting in a similarly low richness in the two types of native plantations.

Though the species pool of grassland specialists (cf. Rédei et al., 2014) is about five times larger in the landscape than that of forest specialists, their richness in the individual plots is moderate, and their occurrence is accidental. They are present in seminatural forests and in established forest plantations with the same low richness, probably because light is the strongest limiting factor for these species, which is similarly deficient in the understory of each established forest type. The continuity of the forest environment is not important for these species. Their good colonization ability in abandoned agricultural areas (Csecserits and Rédei, 2001; Csecserits et al., 2011; Albert et al., 2014; Török et al., 2018) indicates that their propagules may be present in the entire landscape.

Disturbance requiring native weeds were more or less missing in the studied seminatural forests, but their number was high in young plantations, where soil preparation opens colonization windows for them (Heinrichs et al., 2018). Although their number was significantly lower in established plantation forests, where the soil disturbance had ended and the canopy had closed, they subsisted in the forest plantations affected by the earlier disturbance (cf. Kröel-Dulay et al., 2018). The effect of soil preparation and plantation procedure is even more detectable in the presence of alien species. In this group, perennials and woody plants are well represented. In spite of their long life span, most of them are characterized by a good spreading ability and high disturbance tolerance. Similarly to the native weeds, aliens appear in large numbers following clear-felling and soil preparation, but unlike weeds they are not suppressed during succession. They survive and reach significant cover values in forest plantations, making these stands a hotspot of alien species (Csecserits et al., 2016). These results contradict other studies where richness and abundance of aliens declined during secondary succession in plantation forests (Brockerhoff et al., 2003; Schmidt, 2005; Newmaster et al., 2011; Duguid and Ashton, 2013).

4.2. Occurrence of the forest specialists

Our results show that forest specialists are most affected, simultaneously by both the dominant tree species and the management type of the habitat. This group is the most sensitive to every change (Newmaster et al., 2007; Heinrichs et al., 2018), and its survival is related strongly to the continuous cover of seminatural oak forests. Since plantations in the region are established after mechanical site preparation, the resulting strong soil disturbance and the removal of the topsoil, as well as the absence of propagules and the low colonization ability of forest specialist species (Matlack, 1994; Ehrlén and Eriksson, 2000; Verheyen and Hermy, 2004), are presumably the main reasons for the lower richness of specialists in plantation forests. They are nearly absent in young plantations, which shows that clear-felling and mechanical site preparation remove them almost completely from the habitats (Newmaster et al., 2011). If we regard young plantations and established plantation forests as a time series (Brockeroff et al., 2003), the low number of forest specialists in all types of old plantations shows that these species have very limited recolonization ability, at least on this decades-long timescale (Kelemen et al., 2014). We have no data on the possible recolonization in plantations on a longer timescale in our study area, but according to Dupouey et al. (2002), the effect of disturbance could remain even on a millennial timescale.

Forest specialists are present only in limited numbers in native poplar dominated forests, with similar richness in both management types: seminatural and old plantation stands. Because of the relatively short life span of the dominant tree, semiatural poplar stands are a temporally changing mosaic of closed and open poplar woodlands and dry grasslands (Erdős et al., 2018b). Therefore, only the most stress tolerant and well-spreading forest specialists (e.g. *Brachypodium sylvaticum, Geum urbanum*) can be found in poplar stands.

We found that not the examined environmental factors, but rather the dominant tree species of the plantation was the most important factor determining the richness of forest specialists in plantations. Among the landscape level factors, the long-term continuous presence of seminatural oak forests in the surrounding landscape proved to be most vital in fostering their recolonization of plantations (Fig. 5). It shows the importance of the remaining seminatural oak stands as refuges for forest biodiversity (cf. Heinrichs et al., 2018): If permanent seminatural forests are missing from a landscape, there is no chance for a spontaneous regeneration of forest species, because their propagules are absent (Lee et al., 2005; Martin-Queller and Saura, 2013). In such landscapes, we found that the species pool of plantation forests were composed mainly of grassland generalists and alien species. These plantations are unsuitable for (even partially) regenerating the original plant biodiversity, which may have a negative effect on the diversity of other taxonomical groups.

There were nine plots in which we detected moderate richness in the plantations without permanent cover of seminatural forests in the landscape, but these plots were located on the westernmost and most humid subregion of the Kiskunság, with above 580 mm of yearly precipitation. We suppose that due to the more humid climate, the landscape here can be more permeable for the forest specialists, and the gallery forests of the nearby floodplain of the River Danube can continuously provide propagules.

Half of the forest specialists appear exclusively in seminatural oak forests, and the majority of the other half, too, prefers these forests. Consequently, these species disappear forever if the habitat's continuity in time is broken. Only some species have a chance to survive the soil disturbance using rhizomes and in soil seed banks or can recolonize effectively by zoochory or anemochory.

All specialists, except for three disturbance tolerant ones, avoid all types of alien plantations. If the extent of alien plantations in the landscape reaches a critical proportion, they will isolate the natural forest stands and native plantations from each other. This can seriously limit the permeability of the landscape for forest specialists, hindering their recolonization.

5. Conclusions

The key finding of our study is that land use history and the planted tree species jointly determine the species richness and composition of the herb layer of forests in the studied lowland sand region. The management type of the forest (seminatural vs. plantation) seems more important than the identity of the dominant tree species in maintaining plant biodiversity in these forests. We found that forest specialist herbs hardly colonize plantation forests in the forest steppe region; thus, forest specialists are the most vulnerable species group to every change in land use, and their presence can be an indicator of the naturalness of the forests (Newmaster et al., 2007; Heinrichs et al., 2018).

Due to the limited recolonization ability of these species, even the remnants of the local forest flora can completely disappear from the landscape if the current forestry management practice continues. Biodiversity of forests in the forest steppe biome seems to be more vulnerable, and the recolonization of the species is slower than found in earlier studies inside the forest zone (cf. Halpern, 1989; Brunet and von Oheimb, 1998; Wulf, 2004). In the forest steppe region, colonization ability of forest specialists for grasslands is very low (Csecserits et al., 2011); consequently, the landscape with large natural and secondary grasslands is impermeable for them. The remaining natural forest stands are strongly fragmented, probably pledged with a significant extinction debt (Hanski and Ovaskainen, 2002; Vellend et al., 2006; Noh et al., 2018; Heinrichs et al., 2018).

To retain at least some remnants of the original biodiversity of these forest steppe forests, all of the remaining seminatural forests in the region should be protected, without any compromises, as sources of propagules. Where the species pool is still available, the management of the surrounding stands should focus on restoration, defragmentation, and controlling the spread of alien species. Seminatural forests destroyed by natural disasters, such as fires, storms, or frost, should be replaced by native plantations (Bremer and Farley, 2010) using moderate soil disturbance techniques. In this case, if site preparation is inevitable, because saplings would not survive without it, species rich patches of the herb layer should be left undisturbed. In case of any type of management activity, invasion control is necessary. We are in the 24th hour to preserve this element of regional biodiversity.

CRediT authorship contribution statement

Tamás Rédei: Conceptualization, Methodology, Investigation, Data curation, Writing - original draft. **Anikó Csecserits:** Formal analysis, Data curation, Writing - review & editing, Visualization. **Barbara Lhotsky:** Investigation, Writing - review & editing, Project administration. **Sándor Barabás:** Investigation. **György Kröel-Dulay:** Investigation. **Gábor Ónodi:** Investigation. **Zoltán Botta-Dukát:** Methodology, Formal analysis, Writing - review & editing, Funding acquisition.

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.

Acknowledgements

Funding: This work was supported by Hungarian Scientific Research Fund [grant numbers: No. NKFP6/013/2005 and CNK80140]. ACs was funded by the Hungarian Academy of Sciences (MTA, PD-009/2017 and FK128465). TR, ACs, BL, GyKD and ZBD were funded by the GINOP-2.3.2-15-2016-00019 grant.

We would like to thank the several surveyors for field data collection. We also thank Eszter Lelleiné-Kovács and Ildikó Pándy for the GIS work. Finally we thank the three anonymous reviewers for their help to improve the quality of our manuscript.

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