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Native and alien poplar plantations are important habitats for terrestrial orchids

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Abstract: Poplar monocultures are some of the most common short-rotation coppices. While they are most often considered of low environmental value, they have recently gained recognition for their multifaceted role in ecological engineering, such as carbon sinks, soil remediators or green energy producers. Nonetheless, the biodiversity of poplar plantations remains little known and largely overlooked. Here we conducted a systematic botanical survey of 232 poplar plantations within the Pannonian ecoregion (central Europe) in order to assess their plant diversity, with particular focus on terrestrial orchids. Our results highlight that almost 60% of poplar monocultures harbour terrestrial orchids, some with several thousand specimens. Overall, we documented the occurrence of 15 species of terrestrial orchids in the surveyed plantations, including taxa with limited distributions and a threatened conservation status. For instance, we report numerous new populations of *Epipactis bugacenis* and *E. tallosii* in poplar plantations, suggesting that the majority of these taxa occur in poplar monocultures within Hungary. We analysed and highlight soil chemistry and plantation characteristics that predict the occurrence and species richness of terrestrial orchids in poplar monocultures. The probability of orchids being present is highest in older and larger poplar plantations, characterized by high total organic matter content and high soil pH. We conclude that plantations of native and alien poplar harbour valuable plant communities, including terrestrial orchids and other vascular plants of significant conservation importance. Using the knowledge generated here, we recommend delaying or partial harvest of poplar plantations to increase their conservation potential.

Keywords: agroforestry, anthropogenic habitats, biodiversity conservation, *Cephalanthera*, *Epipactis*, *Orchidaceae*, poplar monocultures, vascular plants

Introduction

Poplar trees are widely cultivated as it is one of the most commonly used woods in the construction industry, carpentry, paper production and various other manufacturing industries (Heilman 1999). Due to increasing demands, the number of poplar plantations,

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as well as their acreages are increasing rapidly, especially in the USA, China and South Korea. The International Poplar Commission (1992) listed 19 countries with plantations of at least 10,000 hectares. Seven of these countries (China, France, Germany, Hungary, Romania, Turkey and the former Yugoslavia) harbour more than 100,000 hectares of poplar forests. Poplar is most frequently grown as short-rotation coppice, providing a highly profitable energy crop and is an important arm of agroforestry. To boost the production of traditionally planted, native poplar species, these were gradually replaced by clones of alien hybrid poplars, due to their favourable characteristics. These hybrids have generally high tolerance of harsh environmental conditions, are more resistant to pests and diseases and have shorter production cycles, reaching a large size in considerably shorter time (Laureysens et al. 2005).

Commercial poplar monocultures have long been the centre of attention due to their high economic value. Nonetheless, poplar plantations have recently gained further attention in many countries for their environmental benefits. They are now widely recognized as an efficient system for fixing energy that could partially replace fossil fuels (Isebrands & Karnosky 2001, Hedenus & Azar 2009) and a way to increase soil carbon content and remediate degraded soils (Dewar & Cannell 1992, Block et al. 2006). Poplar plantations may mitigate the harmful effects of CO_2 emissions (e.g. greenhouse effects) on the environment (Arevalo et al. 2011, Rytter 2012). Moreover, establishing short-rotation poplar plantations in dry areas is an efficient way of restoring degraded habitats (Sartori et al. 2007). Nonetheless, despite their ever-increasing area and economical importance, the effect of poplar monocultures on local biodiversity has rarely been studied and is little understood. Timber producing monocultures are generally considered to be habitats with low biodiversity, uncharacteristic herbaceous plant layer and dominated by alien species. Consequently, poplar monocultures are often referred to as a "green desert" and the natural values of these forests are currently remarkably underrated. According to the book on Hungarian habitats, poplar plantations are of little environmental value (Bölöni et al. 2011).

Contrary to these remarks, a recent systematic evaluation of biodiversity in planted poplar and willow forests in Sweden, highlighted the potential of these habitats to harbour a significant diversity of plants (Baum et al. 2012). While energy-producing monocultures are a threat to biodiversity, the harm caused by poplar plantations is likely to be much lower (Fletcher Jr. et al. 2010) than that of other energy crops (e.g. maize, soybean). For instance, a study conducted in the UK concluded that contrary to most widely cultivated adventive tree species, the herbaceous plant layer in poplar plantations is generally well-developed, resulting in an overall valuable and diverse flora, potentially offering favourable conditions for a more diverse fauna (Sage & Robertson 1994). Although the species composition and conservation value of tree plantations can be significantly influenced by various factors such as the history of land use, tree planting and management practices, plantations can be differentiated according to whether the planted species are indigenous or introduced (see Bölöni et al. 2011). Orchids are ideal bioindicators of anthropogenic habitats, mainly due to their high diversity, their conservation importance and likelihood to colonize anthropogenic habitats, e.g. abandoned mines (Jurkiewicz et al. 2001, Esfeld et al. 2008, Shefferson et al. 2008); cemeteries (Löki et al. 2015, 2019, Molnár V. et al. 2017b); roadside verges (Fekete et al. 2017, 2019, 2020). Terrestrial orchids are repeatedly documented as occurring in various plantations, including coffee (Solis-Montero et al. 2005), cocoa (Morales-Linares et al. 2020) and rubber (Madison

Fig. 1. Poplar plantations are widespread in agriculturally intensively used landscapes on the Great Hungarian Plain. (A) Bird's eye view of poplar plantation of different ages surrounded by arable fields (Ricse, photographed by L. Simán). (B) Mass occurrence of the orchid white helleborine (*Cephalanthera damasonium*) in a hybrid poplar monoculture (Hajdúböszörmény, photographed by A. Molnár V.).

1979), but also long-established cultures such as olive groves (Vuković et al. 2011, Molnár V. et al. 2017a) and chestnut orchards (e.g. Croce & Nazzaro 2012). The first reports of orchids in poplar plantations are from Poland (Adamowski & Conti 1991), where three orchid taxa (*Dactylorhiza incarnata*, *Epipactis helleborine* and *Platanthera bifola*) are reported in a single poplar plantation. There is also floristic data on the occurrence of orchids in poplar plantations in Hungary (Csábi et al. 2015, Aradi et al. 2017, Illyés et al. 2017, Lukács et al. 2017, Süveges et al. 2020, Süveges 2022), where they regularly harbour large populations of *E. tallosii* (Süveges et al. 2019). A recent review of this topic found evidence of the presence of orchids in poplar monocultures in 16 European countries and for 32 orchid taxa (Molnár V. et al. 2022).

The establishment and colonization success of terrestrial orchids in anthropogenic and disturbed habitats is believed to be related to their dispersal ability (Arditti & Ghani 2000), as well as their tolerance of stress (S) and/or ruderal (R) strategy (Pierce et al. 2014). Fruits of orchids contain thousands of 'dust seeds' (Barthlott et al. 2014, Sonkoly et al. 2016), suggesting that they are able to colonize new habitats through anemochorous seed dispersal and utilize resources at distant sites.

Evidence recently started to accumulate that indicates poplar monocultures (Fig. 1) are important habitats for terrestrial orchids. Nonetheless, there is little information on which taxa are able to colonize these habitats and the size of their populations. Here we report the results of a systematic survey of poplar monocultures across Hungary with the primary aim of exploring (i) the diversity and taxonomic composition of orchids colonizing poplar plantations, and to (ii) identify characteristics of poplar plantations (naturalness of planted poplar taxa, soil chemistry, trunk diameter, average distance between trunks) that are associated with their suitability for orchids.

Materials and methods

Field work

Field work was carried out from July to September in six consecutive years (from 2014 to 2019), within Hungary and its bordering regions (see Supplementary Table S1). In Hungary, poplar plantations are largely restricted to lowland areas, therefore highlands and montane regions were generally avoided during field surveys. Poplar plantations were randomly selected either on a priori basis using satellite images or were spotted randomly while driving along public roads. We aimed to sample plantations of various ages (based on visual inspection of the diameters of poplar trunks) and in various landscapes, but avoided very young plantations (i.e., average trunk diameters < 9 cm) and ploughed plantations. Systematic surveys were carried out in 232 poplar plantations in Hungary (219) and close to the Hungarian borders in Romania (3), Serbia (3), Croatia (3) and Ukraine (4). In each of these plantations, we recorded the following abiotic information: (i) geocoordinates and (ii) altitude (i.e. height above sea level) using a handheld GPS device. Moreover, in every plantation, we recorded (iii) the diameter of the trunks of ten randomly selected poplar trees, which was measured at a height of 130 cm above the ground, using a measuring tape. In order to quantify tree density, we also measured (iv) the distance between 10 randomly selected trees and their closest neighbouring tree using a measuring tape (see Supplementary Table S1). The average distance of the latter

10 measurements was calculated and used as a measure of tree density in the plantations, for which the smaller the value the denser the plantation. Furthermore, we surveyed each plantation for orchids by searching the whole of each plantation and recording (v) the presence, abundance (by counting/estimating the total number of individuals) and species of all the orchids detected. Taxa were identified based on Delforge (2006) and the nomenclature used follows Molnár V. & Csábi (2021). Furthermore, at each location we also recorded the naturalness of the poplar trees present in the plantation. We used two categories: native (mixed plantations, which contain both native and alien poplar trees, n = 31) and alien plantations (n = 201). Poplar taxa were identified following Bartha (2009). *Populus alba*, *P. ×canescens*, *P. nigra* and *P. tremula* were considered to be native and *P. ×euramericana* alien. In 185 plantations, we also collected soil samples (i.e. 1 kg) at the root-depth (5–15 cm) of orchids from five different locations (~200 grams each) within a plantation for subsequent laboratory analyses. Soil samples from each plantation were mixed thoroughly before laboratory measurements and analysed in the accredited laboratory of the Research Institute of Karcag of the Hungarian University of Agriculture and Life Sciences. The following seven parameters were measured: pH (KCl), total soluble salt content (m/m%), $CaCO_3$ content (m/m%), total organic matter content (m/m%), available nitrogen (mg/kg), available phosphorus (mg/kg) and available potassium content (mg/kg). Nitrogen content (in NO_3 and NO_2 form) was extracted in 1 M KCl-solution and determined by spectrophotometry after reduction of NO_3 to NO_2 in a Cd column. In the case of phosphorous and potassium we used ammonium-lactate solution. AL-soluble phosphorus (AL-P_2O_5) content of soils was determined by spectrophotometry, while AL-soluble potassium (K_2O) content was determined by atomic absorption spectrophotometry. Following field work, we also measured the total area of each plantation surveyed using satellite images provided by the Google Earth Pro software (matching the year of survey of each plantation).

Data analyses

In order to assess which characteristics of poplar plantations define their suitability for orchids we constructed generalized linear models using package stats (function glm) for presence/absence of any orchid taxa and the number of species detected in each plantation, with binomial or Poisson error distributions, respectively. Each data point was based on a single surveyed poplar plantation. Given that soil chemistry was not available for all the plantations surveyed, we ran each model in two steps. First, we ran models using predictors describing characteristics of the poplar plantations that were measured at every location surveyed (n = 232). These predictors included plantation area, altitude, naturalness of the poplar forest (native/alien), average trunk diameter (within plantation variance in trunk diameter was also tested, but was not correlated with either orchid presence or number of species, results not shown) and average distances between trees. Using stepwise backward selection, based on the largest P value we removed predictors, with a threshold of $P > 0.1$ to obtain a minimum adequate model. Second, only using data on plantations for which soil chemistry was measured (n = 185) we repeated the above minimum models, additionally introducing soil chemistry parameters, including pH, total salt, $CaCO_3$, organic matter, nitrogen, phosphorus and potassium content as predictors. Sample size varied slightly across models, due to incomplete soil chemistry parameters for two plantations. Model selection was carried out again to obtain minimum adequate models. All covariates were scaled and all soil chemistry parameters (except pH) were log-transformed to ensure model residual normality. All statistical analyses and graphical presentations were done using R statistical and programming environment, version 4.0.4 (R Core Team 2021).

Results

Orchid prevalence and diversity

The majority (59.9%) of the poplar plantations surveyed harboured at least one species of orchid (Fig. 2). In all the poplar monocultures, 15 species of orchids belonging to seven genera were recorded (see Fig. 3 for a summary). The most common genera were *Epipactis* and *Cephalanthera*, represented by six and four species, respectively. Two species of *Neottia* and one species of *Anacamptis*, *Orchis*, *Platanthera* and *Ophrys* were also recorded. The number of species of orchids recorded in a single poplar plantation ranged from one to five (Fig. 2). The most widespread species was *Epipactis tallosii* (57 plantations), followed by *Cephalanthera damasonium* (45 plantations) and *E. helleborine* (44 plantations) (Fig. 3). The total number of orchid individuals in a single poplar plantation ranged from one to 10,251 (Fig. 4). The largest number of specimens of a particular species recorded in all the plantations surveyed was for *C. damasonium*, with a total of 18,056 individuals.

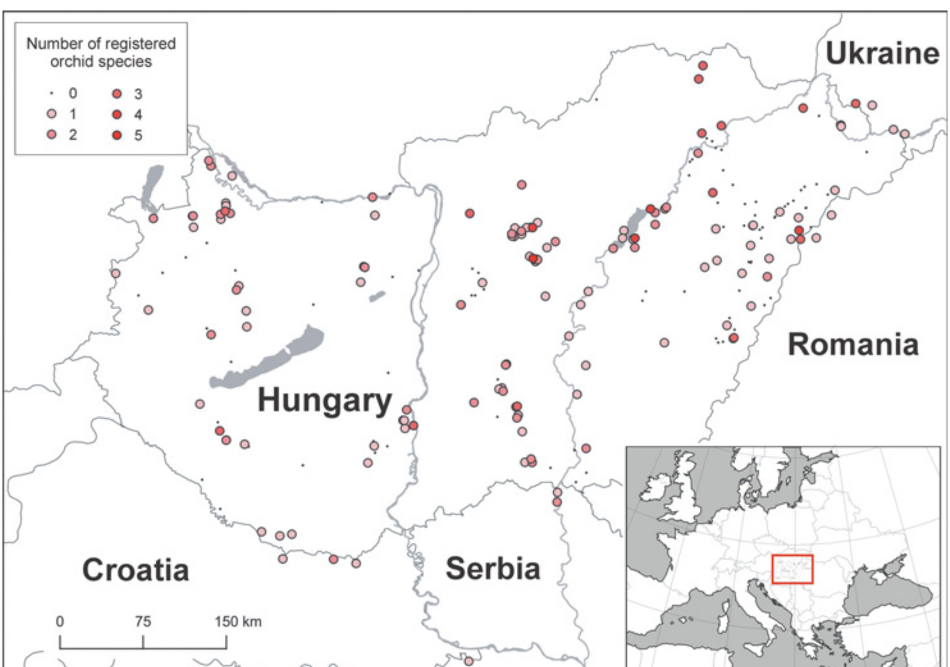

Fig. 2. Map showing the locations of the poplar plantations surveyed and number of species of orchid recorded.

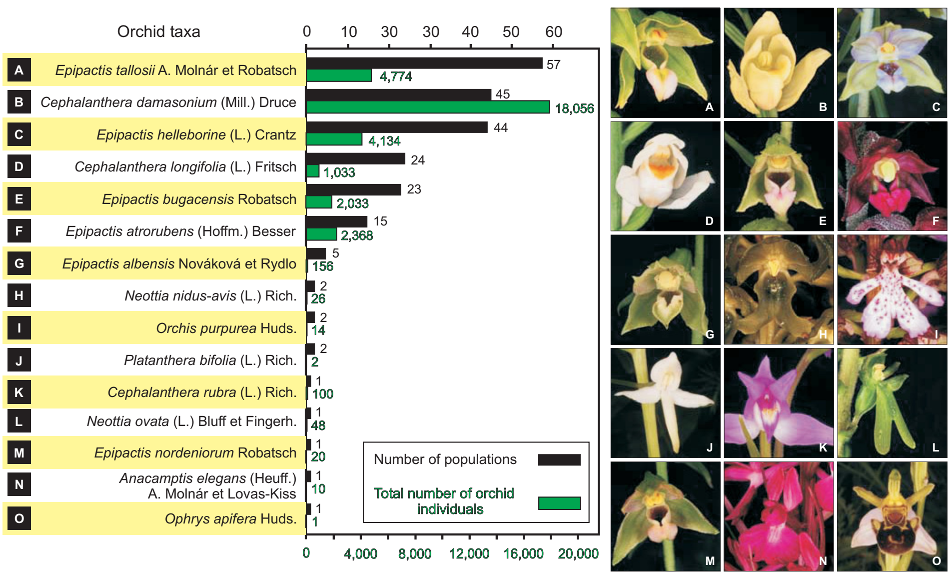

Fig. 3. Summary of the orchid occurrences recorded in the 232 poplar plantations surveyed. The number of plantations in which each species was present (Number of populations), and overall number of individuals (Total number of orchid individuals) are indicated. Photographed by A. Molnár V.

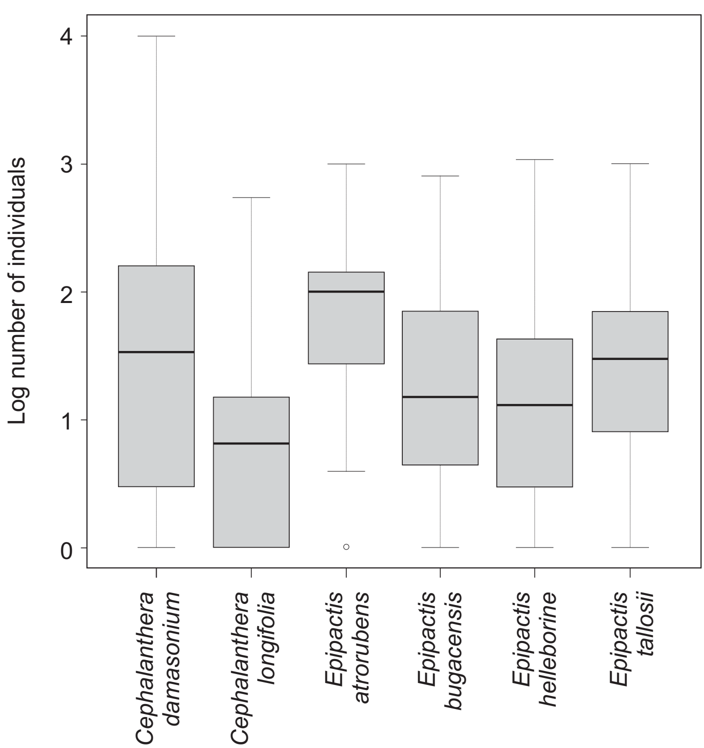

Fig. 4. Population sizes of the six most commonly detected species of orchid in the poplar plantations studied.

Characters of poplar plantations associated with their suitability for orchids

The only significant predictor of orchid presence in poplar plantations was average trunk diameter (Table 1A), indicating a higher likelihood of detecting orchids in plantations in which the trunks of the trees are broader (Fig. 5A). Plantation area correlated positively, while altitude correlated negatively, with the likelihood of orchid presence, but these correlations were not significant. Orchid presence was similar in poplar plantations with different naturalness (i.e. alien vs native). No significant correlation was detected between probability of orchid presence and plantation density based on the average distance between trunks in the plantations. Of the soil chemistry parameters, tested by adding them to the minimum model, only total organic matter and potassium content correlated significantly with orchid presence (Table 1B). The likelihood of detecting orchids in a poplar plantation decreased with increasing potassium content (Fig. 5B) and increased with increasing soil organic matter content (Fig. 5C). Soil pH, nitrogen, $CaCO_3$, salt or phosphorus content correlated insignificantly with the probability of detecting at least one orchid species in individual poplar plantations.

Table 1. Result of binomial GLM regressions exploring the correlation between probability of orchid presence and (A) plantation characteristics and (B) soil chemistry in poplar plantations. Both full (left) and minimum adequate models (right) are shown.

A. Correlation between plantation characteristics

Full model				Minimum model			
	β (SE)	t	P		β (SE)	t	P
Intercept	0.44 (0.17)	2.49	0.0126	Intercept	0.41 (0.16)	2.49	0.0126
Area	0.29 (0.16)	1.82	0.0685	Area	0.27 (0.16)	1.74	0.0823
Altitude	–0.28 (0.15)	–1.84	0.0655	Altitude	–0.28 (0.15)	–1.86	0.0634
Tree naturalness	–0.28 (0.47)	–0.60	0.5478	Average trunk diameter	0.99 (0.20)	4.94	< 0.0001
Average trunk diameter	1.06 (0.22)	4.80	< 0.0001				
Average trunk distance	–0.12 (0.18)	–0.70	0.4865				
Sample size			n = 232	Sample size			n = 232

B. Correlation between soil characteristics

Full model				Minimum model			
	β (SE)	t	P		β (SE)	t	P
(Intercept)	0.31 (0.18)	1.74	0.0824	(Intercept)	0.33 (0.18)	1.88	0.0599
Area	0.12 (0.19)	0.64	0.5231	Area	0.14 (0.18)	0.77	0.4409
Altitude	–0.11 (0.17)	–0.62	0.5359	Altitude	–0.14 (0.17)	–0.81	0.4153
Average trunk diameter	0.37 (0.17)	2.13	0.0328	Average trunk diameter	0.35 (0.17)	2.07	0.0384
Organic matter content	0.94 (0.26)	3.69	0.0002	Organic matter content	0.83 (0.21)	3.90	0.0001
Potassium content	–0.46 (0.27)	–1.67	0.0942	Potassium content	–0.60 (0.21)	–2.88	0.0040
pH	0.48 (0.26)	1.85	0.0650	pH	0.29 (0.16)	1.76	0.0781
$CaCO_3$-content	–0.11 (0.26)	–0.43	0.6682				
Nitrogen content	–0.11 (0.20)	–0.52	0.6017				
Total salt content	–0.21 (0.20)	–1.02	0.3099				
Phosphorus content	–0.19 (0.24)	–0.82	0.4097				
Sample size			n = 184	Sample size			n = 185

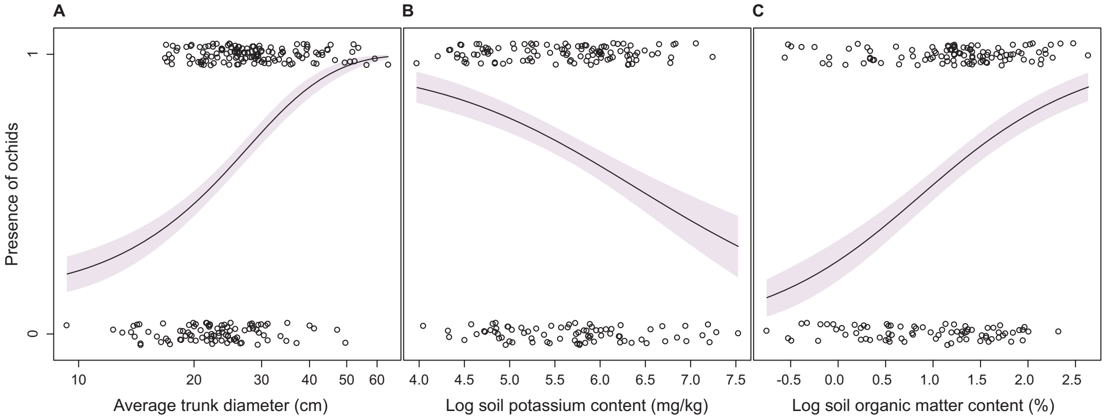

Fig. 5. Association between orchid presence and characteristics of poplar plantations. (A) mean trunk diameter, (B) soil potassium content, (C) soil total organic matter content. Fitted lines and associated standard errors were obtained using the models presented in Table 1. Random noise was added to orchid occurrences to facilitate the visualization of overlapping points.

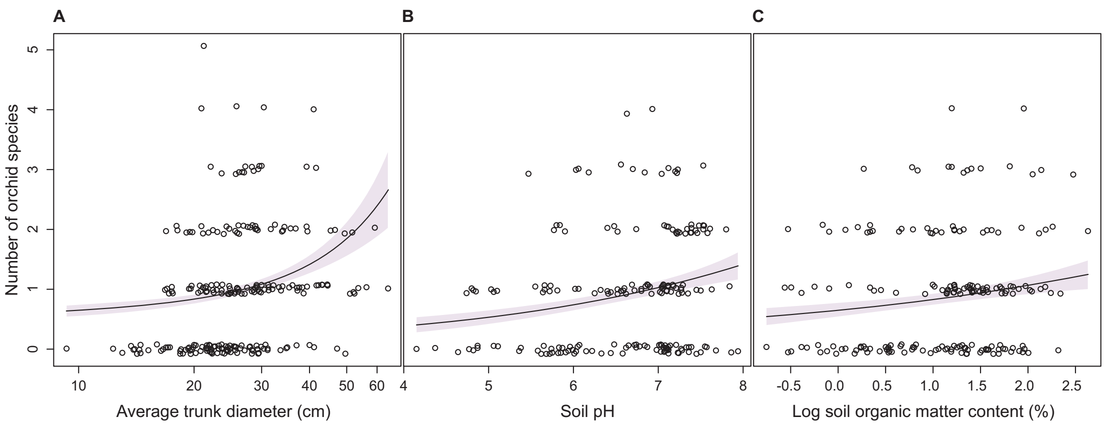

Fig. 6. Association between orchid species richness and characteristics of poplar plantations. (A) mean trunk diameter, (B) soil pH, (C) soil total organic matter content. Fitted lines and associated standard errors were obtained using the models presented in Table 2. Random noise was added to the number of orchid species to facilitate the visualization of overlapping points.

In terms of the plantation characteristics tested, the numbers of species of orchids was significantly positively correlated with average trunk diameter (Fig. 6A) and plantation area (Table 2A). Orchid species richness was similar in poplar plantations that differed in naturalness. The correlation between altitude and orchid species richness in poplar plantations was not significant. Of the soil chemistry parameters tested, only soil pH and soil organic matter content correlated significantly with orchid species richness (Table 2B), indicating more orchid species in poplar plantations with a high soil pH (Fig. 6B) and high soil organic matter content (Fig. 6C). Neither soil phosphorus, salt, potassium, nitrogen or carbonate content correlated significantly with orchid species richness. Correlation matrix of plantation characteristics and soil parameters is available in Supplementary Table S2.

Table 2. Result of poisson GLM regressions exploring the correlation between probability of orchid presence and plantation characteristics (A) and soil chemistry (B) in poplar plantations. Both full (left) and minimum adequate models (right) are shown.

A. Correlation between plantation characteristics							
Full model				Minimum model			
	β (SE)	t	P		β (SE)	t	P
(Intercept)	–0.17 (0.09)	–1.97	0.0490	(Intercept)	–0.18 (0.08)	–2.20	0.0280
Area	0.25 (0.07)	3.33	0.0009	Area	0.22 (0.07)	3.14	0.0017
Altitude	–0.13 (0.07)	–1.71	0.0866	Average trunk diameter	0.24 (0.06)	3.99	0.0001
Tree naturalness	–0.28 (0.21)	–1.32	0.1855				
Average trunk diameter	0.33 (0.07)	4.48	< 0.0001				
Average trunk distance	–0.10 (0.08)	–1.32	0.1876				
Sample size			n = 232	Sample size			n = 232

B. Correlation between soil characteristics							
Full model				Minimum model			
	β (SE)	t	P		β (SE)	t	P
(Intercept)	–0.29 (0.10)	–2.92	0.0035	(Intercept)	–0.25 (0.10)	–2.59	0.0096
Area	0.21 (0.10)	2.14	0.0327	Area	0.18 (0.09)	1.94	0.0521
Average trunk diameter	0.25 (0.07)	3.45	0.0006	Average trunk diameter	0.21 (0.07)	3.05	0.0023
Organic matter content	0.30 (0.12)	2.55	0.0108	Organic matter content	0.18 (0.09)	2.00	0.0458
Potassium content	–0.10 (0.12)	–0.79	0.4270	pH	0.27 (0.09)	2.88	0.0039
pH	0.28 (0.14)	1.93	0.0542	Phosphorus content	–0.16 (0.08)	–1.93	0.0538
$CaCO_3$-content	0.02 (0.13)	0.19	0.8521				
Nitrogen content	–0.15 (0.10)	–1.42	0.1559				
Total salt content	–0.08 (0.10)	–0.82	0.4146				
Phosphorus content	–0.08 (0.11)	–0.72	0.4696				
Sample size			n = 184	Sample size			n = 185

Table 3. Comparison of the percentage of self-pollination in the orchid flora of Hungary and among orchids detected in the poplar plantations surveyed.

	Self-pollinating species	Total	Percentage self-pollination
Number of orchid species in Hungary	23	71	32.4%
Number of orchid species in poplar plantations surveyed	7	15	46.7%
Number of orchid populations in poplar plantations surveyed	135	225	60.0%
Number of orchid individuals in poplar plantations surveyed	25,067	32,776	76.5%

Discussion

This study provided four key results. First, it highlighted the potential of both native and alien poplar monocultures as habitats for important plant communities, especially, rare and protected terrestrial orchids. Second, there are poplar plantations with very high numbers of orchid specimens, some with over ten thousand individuals, reaffirming that poplar plantations provide good conditions for the establishment and reproduction (as suggested by occasional high densities) of at least certain orchid taxa. Third, a significant portion of the narrowly distributed *Epipactis bugacenis* and *E. tallosii* populations occur in poplar plantations. Fourth, some characteristics (e.g. trunk diameter, soil total organic matter or potassium content and soil pH) of poplar plantations are associated with their suitability for terrestrial orchids.

Orchids colonizing poplar plantations

The presence of at least one species of orchid was recorded in almost 60% of the poplar plantations surveyed, indicating that the colonization of poplar plantations is a frequent and widespread phenomenon. The conservation importance of poplar plantations is further supported by the fact that some of the orchid populations recorded were very large and consisted of thousands of flowering specimens. Moreover, numerous species of orchids recorded during the surveys (e.g. *Epipactis bugacensis*, *E. tallosii*, *E. nordeniorum*) are widely acknowledged to have small distributions (Delforge 2006), which reaffirms the importance of poplar monocultures as potential refugia for threatened orchids.

A total of 225 orchid populations, belonging to 15 species were recorded in the poplar plantations. Most of the populations (96%) were of the genera *Epipactis* (146 populations) and *Cephalanthera* (70 populations). These two genera are taxonomically closely related members of the *Epidendroideae* subfamily, are both rhizomatous and can colonize distant and anthropogenically influenced habitats (Dickson 1990, Hollingsworth & Dickson 1997, Jurkiewicz et al. 2001, Esfeld et al. 2008, Shefferson et al. 2008, Kotilínek et al. 2020). In addition to dispersal by seed, their establishment is associated with ectomycorrhizal fungi (Ouanphanivanh et al. 2008, Schiebold et al. 2017): *Epipactis* mainly pezizalean ascomycetes (Těšitelová et al. 2012), *Cephalanthera* a wider taxonomic range of fungi (Pecoraro et al. 2017). It is likely that the establishment of these orchids in poplar plantations is aided by the large ectomycorrhizal diversity characterizing the root zone and soils of poplar plantations, irrespective of the genotype of *Populus* (Danielsen et al. 2012, 2013).

Interestingly, the majority of the orchids recorded in poplar plantations are self-pollinating species (Table 3). This might be an important factor as most poplar plantations are located in intensely managed agricultural land. The low biodiversity in agricultural monocultures (Krebs et al. 1999), frequent use of pesticides and limited food resources for insects (Stuligross & Williams 2020) might limit the diversity of potential pollinators in poplar plantations. Self-pollinating species are largely independent of insects, which is likely to account for their greater abundance in poplar plantations than insect-pollinated orchids.

Plantation characteristics associated with orchid presence and diversity

Island biogeography theory predicts that a greater number of species are likely to be recorded in habitats of large spatial extent. Nevertheless, plantation area did not explain orchid presence, but was positively associated with the number of species of orchids. The latter indicates that large poplar plantations are likely to harbour a more diverse terrestrial orchid community than small ones. Trunk diameter is another significant predictor of both orchid presence and species richness, with plantations with a large average trunk diameter most likely to harbour many species of orchids. The reason for this is likely to be twofold, both connected with the fact that a large trunk diameter indicates that the plantation is old. First, if a plantation is old it has been present for a sufficiently long time for orchids to colonize and become established and reproduce, which results in an increase in both their detectability and abundance. A similar trend is reported for vascular epiphytes in shaded coffee plantations (Richards et al. 2020). In addition, our result is also supported by the observation that the diversity of plants recorded in these plantations increases with the age at harvesting (Archaux et al. 2010). Second, the species richness of ectomycorrhizal associations is strongly correlated with the age of the trees (Tóth & Barta 2010), which is likely to benefit the establishment of mycorrhiza-dependent orchids. In addition, orchids were recorded in poplar plantations with average trunk diameters between 16.8 and 64.1 cm. Poplar reaches a trunk diameter of 21–30 cm in about 22 years (Radó 1999). Poplar in plantations is harvested between 18–25 years for timber production and between 15–18 years for chip-wood and paper manufacture (Rédei 2010). The earliest orchids appear aboveground is (4–) 7–8 years (Archaux et al. 2010, Tullus et al. 2015, Molnár V. et al. 2022). Young poplars are sensitive to understory growth, which significantly retards their growth and productivity (Heilman 1999). Therefore, management practices in young plantations often include the use of herbicide and ploughing, which decreases the probability of orchids becoming established.

High soil organic matter content was positively correlated with orchid presence and species richness in poplar plantations. This correlation is likely to be indirect, as orchids rely on fungi for a supply of carbohydrates, especially in their early stages of development (Schweiger et al. 2018). Nonetheless, ectomycorrhizal fungi use soil organic matter as a source of organic nitrogen and the availability of soil organic matter is likely to correlate with the abundance of ectomycorrhizal fungi (Lindahl & Tunlid 2015, Shah et al. 2016). For instance, McCormick et al. (2012) report that the addition of organic matter improves the germinability of two out of the three species of terrestrial orchids by affecting the abundance of host fungi. Moreover, while some studies report a positive (Batty et al. 2001, Bichsel et al. 2008) or neutral correlation (Dijk & Olff 1994) between potassium and orchid performance, our results indicated a negative correlation.

Conservation relevance

While not the primary focus of the present study, we also recorded the occurrences of species of vascular plants of conservation importance. We documented populations of plant species protected by Hungarian law (numbering of locations, which follows that in Supplementary Table S1, are in parentheses): *Allium carinatum* (187); *Cnidium dubium* (160); *Dianthus serotinus* (101); *Dryopteris carthusiana* (130, 145, 189); *Iris sibirica* (187); *Ornithogalum brevistylum* (63); *Polystichum aculeatum* (91); *Pseudolysimachion longifolium* (55); *Sonchus palustris* (75, 151) and *Stipa borysthenica* (103).

Our systematic survey revealed rare/ uncommon plants in poplar plantations, highlighting the contribution of these plantations to local biodiversity and species conservation. Orchids are considered to be umbrella species because of their specific biology (Molnár V. 2011), thus their presence may be correlated with the presence and/or species richness of several other groups of organisms, but this needs further study in the case of poplar plantations. Seven of the species of orchids detected in poplar plantations are on the Hungarian Red List (Király 2007). Moreover, *Epipactis noredeniorum* is listed as vulnerable and *E. tallosii* as an endangered species on the IUCN Red List. Nevertheless, it was recently proposed that *E. tallosii* should be removed from these lists, due to the significant populations recently reported in poplar plantations (Süveges et al. 2019). Since all orchids are protected by law in Hungary, the conservation significance of poplar plantations is evident. Nonetheless, it is worth noting that poplar plantations are artificial, anthropogenic habitats, that harbour significantly lower biodiversity compared to natural forests. Consequently, we strongly advocate against the destruction of natural habitats in order to create poplar monocultures. The knowledge generated here, however, could be used to aid conservation, especially of terrestrial orchids with highly restricted distributions. While the primary economic reason for the existence of these plantations greatly restricts their potential for conservation, slight alterations in their management might increase their conservation potential, without significantly limiting the economic profit of these plantations. Future studies should explore the trade-off between economic and conservation effects of the following: (i) preference for log production instead of biomass production and so increasing the age of the plantations; (ii) promoting spatial mosaics of different aged plantations, which would facilitate the colonization of such plantations by anemochorous orchids; (iii) abandonment of inter-row tillage of plantations after 1–2 years; (iv) ban or limit the use of herbicide.

Conclusions

Poplar plantations, irrespective of their naturalness, are important habitats for terrestrial orchids. This highlights the importance of poplar plantations compared to other alien tree plantations, in nature conservation. Many of the threatened species of plants recorded in these plantations are on Red Lists, including numerous species of orchids. Furthermore, the overwhelming majority of the Hungarian populations of some of the orchids occur in poplar plantations. While plantations of other alien trees (e.g. *Robinia pseudoacacia*) are often associated with serious decreases in diversity and significant changes in local species composition (Benesperi et al. 2012), poplar plantations appear to be beneficial not only for orchids, but also for local biodiversity in general (e.g. Lust et al. 2001, Martín-García et al. 2016). Based on our results, large and old plantations of poplar characteristically had higher soil total organic matter contents, higher soil pH and lower soil potassium content and the highest conservation potential for forest dwelling orchids.

Supplementary materials

Table S1. – Numbering, year of observation, location, altitude, orchid and poplar taxa, soil parameters, diameters and distances of trunks in the 232 plantations studied.
Table S2. – Correlation matrix of plantation characteristics and soil parameters.
Table S3. – Model results (performed separately for the six most common species) showing the correlation between plantation characteristics and orchid presence, and soil chemistry and orchid presence.

Supplementary materials are available at www.preslia.cz

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Původní i nepůvodní topolové výsadby jsou důležitým stanovištěm pro suchozemské orchideje

Topolové monokultury patří k nejběžnějším porostům s krátkou dobou obmýtí. Přestože jsou z environmentálního hlediska obecně považovány za málo hodnotné, v poslední době se začíná oceňovat jejich role v ukládání uhlíku, remediaci půdy či produkci zelené energie. Biologická rozmanitost topolových výsadeb však zůstává málo známá a do značné míry přehlížená. Provedli jsme systematický botanický průzkum 232 topolových výsadeb v Panonském ekoregionu (střední Evropa) s cílem posoudit jejich rostlinnou diversitu, se zvláštním zaměřením na suchozemské orchideje. Naše výsledky ukazují, že v téměř 60 % topolových monokultur rostou suchozemské orchideje, některé v několika tisících exemplářích. Celkem jsme ve studovaných výsadbách nalezli 15 druhů orchidejí, včetně ohrožených taxonů s omezeným rozšířením. Zaznamenali jsme například četné nové populace *Epipactis bugacenis* a *E. tallosii*. Pravděpodobnost výskytu orchidejí je nejvyšší ve starších a větších topolových porostech, které se vyznačují vysokým obsahem celkové organické hmoty a vysokým pH půdy. Ukázali jsme tedy, že výsadby původních i nepůvodních topolů hostí cenná rostlinná společenstva, včetně suchozemských orchidejí a dalších cévnatých rostlin významných z hlediska ochrany přírody. Na základě získaných poznatků doporučujeme postupy těžby topolových kultur (postupná či odkládaná těžba), které mohou zvýšit jejich ochranářský potenciál.

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