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ORIGINAL PAPER

Tree species diversity facilitates conservation efforts of European yew

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Abstract

European yew (*Taxus baccata*) is an endangered long-lived tree species. The species is facing a regeneration failure in a large part of its natural distribution, likely due to interplay of climate change and browsing by herbivores. Forest management approaches that support inter-specific complementarity can help the species mitigate these negative effects. However, a lack of long-term records has prevented an adequate answer to the facilitation hypothesis. Therefore, we compiled unique data from eleven long-term plots established on three sites in the western Carpathian Mountains in 1972, 1989 and 1995. During the past 30–50 years, forest stands were treated by various management alternatives, and the development of stands and regeneration were monitored in 5–12-year intervals. In this study, we tested the hypothesis that an increase in tree species diversity positively correlates with abundance of yew regeneration. Additionally, we compared the relationships between management and no-management alternatives. Our results revealed the positive correlation of tree species diversity and the quantity of yew regeneration. Moreover, an increase in the proportion of maple seedling at the expense of beech supported the establishment of yew seedlings at increased abundance. However, recently (since 1982) the growth of yew saplings did not exceed 20 cm in height, mostly because of heavy damage caused by deer browsing. We conclude that forest managers and conservationists can support the regeneration of yew using the treatments that increase tree species diversity.

Keywords Deer browsing · Forest dynamics · Forest management · Inter-species competition · Long-term observations · Nature reserve

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Introduction

European yew (*Taxus baccata*) is a threatened species (IUCN Red List; Farjon 2013) that is native to western, central and southern Europe, northwest Africa, northern Iran and southwest Asia (Benham et al. 2016). The species has experienced a sharp decline, as one of the most endangered European tree species (Korpeľ 1995; Paule et al. 1996; Svenning and Magård 1999; Thomas and Polwart 2003; Thomas and Garcia-Martí 2015). Yew is now protected, and forests that harbour it have been designated special protected areas included in the EU Habitats Directive. Although protected, the species faces additional pressure as a source of taxane alkaloids used for cancer-treating pharmaceuticals (Jennewein and Croteau 2001).

In conservation decisions and strategies, the time frame of 100 years is commonly used (Wood and Gross 2008). In this period, populations of long-lived tree species, even when lacking regeneration, often do not undergo substantial declines and therefore receive little attention in conservation plans (Kwit et al. 2004). Yew suffers from a lack of regeneration, high seedling mortality and the inability of recruitment to develop beyond a sapling growth stage across a large part of the distribution area. The lack of light and low temperature together with herbivory and seed predation by rodents are the likely factors limiting the regeneration of yew in the northern and eastern parts of the geographic range of the species (Hulme 1996; Svenning and Magård 1999; Iszkuło and Boratyński 2005; Perrin et al. 2006; Dhar et al. 2007; Farris and Filigheddu 2008; Sedmáková et al. 2018). In the Mediterranean, water availability is the primary driving factor (Mendoza et al. 2009; Linares 2013; Romo et al. 2017).

Interactions between canopy trees and yew recruitment have several aspects. Interactions among the species of the same trophic level beneficial to yew recruitment, or facilitation, occur through direct (altering the physicochemical environment) or indirect (mediated by a third organism) mechanisms (Bertness and Callaway 1994; Calaway 1995; Callaway and Walker 1997; Mcintire and Fajardo 2014). For example, the tree species composition of the forest canopy can be directly important. In the broadleaved-dominated forests, earlier spring photosynthetic activity of yew recruitment has been observed, resulting from the higher light availability in the period before the leaves development of the canopy trees (Iszkuło and Boratyński 2004; Pietzarka 2005; Iszkuło 2010). Species diversity can have also an indirect positive effect on recruitment because of an increase in regeneration niches in species-rich forests (Grubb 1977) and possible attraction of more seed dispersers and/or protection from damage by herbivores (García et al. 2000; García and Obeso 2003; Farris and Filigheddu 2008). Hence, the abundance of yew recruitment can be higher in mixed-species than that in yew-dominated forests (Casals et al. 2015). On the other hand, the intra-specific competition between adult yew trees and regeneration may turn to negative effects limiting the establishment and growth of new seedlings (Dovčiak 2002; Piovesan et al. 2009; Devaney et al. 2018). According to Janzen–Connell hypothesis, the conspecific negative effects are distance, density or size dependent (Janzen 1970; Connell 1971; Comita et al. 2014; LaManna et al. 2017). The theory also predicts that higher biodiversity can be maintained by interactions among tree species and their natural enemies. Regarding yew population in Slovakia, deer species can be considered as one of the natural enemies (Sedmáková et al. 2017) that can help maintain or increase tree species diversity. The relative importance of tree species interactions affecting yew seedling survival changes over time (Yan et al. 2015). In later life stages, light demand of yew may become dominant factor, and seedlings are likely to experience high mortality rates when light availability is lacking. Such relationships are then reflected in the spatial arrangement of yew recruitment. Locally, high density of mature yew trees suppresses yew regeneration and therefore becomes a limiting factor, whereas the more scattered occurrence of large, mature trees has a positive effect on regeneration (Piovesan et al. 2009).

Although yew, as an endangered tree species in Europe, has received more attention in conservation activities, the knowledge about conservation management is limited. Slow growth, delayed reproduction, and extraordinarily long lifespan suggest that yew requires long-lasting stable ecological conditions. Natural beech forests in which small-scale disturbances drive the recruitment of trees can provide such stable conditions (Kucbel et al. 2012). Management interventions (thinning and cutting methods) can help prevent yew suppression from high beech competitive pressure by mimicking small-scale disturbances. Long-term experiments show that appropriate management can support development and diversity of natural regeneration of forest trees (e.g., Barna and Bosela 2015; Dobrowolska et al. 2017). The failure of yew to regenerate has been repeatedly documented. In the northern part of Europe, dense canopy is supposed to limit yew recruitment (e.g., Svenning and Magård 1999; Iszkuło et al. 2005); however, because of a lack of relationship between canopy closure and the density of yew regeneration, additional factors likely play a role (Dhar et al. 2007). The past investigations show that high species diversity helps European yew mitigate the regeneration failure. However, the facilitation hypothesis has not been satisfactorily investigated simply because of a lack of long-term experiments.

For the first time, according to our knowledge, we used unique long-term experiments established in the western Carpathians to gain a better understanding of the effects of tree species diversity, different management practices and stand structure on the natural regeneration of European yew. We tested the following hypotheses:

H1 High tree species diversity does not significantly correlate with quantity of yew regeneration in the beech-dominated forests in central Europe.

H2 Forest management, modifies the relationship between species diversity and abundance of yew regeneration.

Materials and methods

Study area and historical background

For this study, we selected three research objects, which were nature reserves (NR) with occurrence of European yew in the western Carpathians, Slovakia (Table 1, Fig. 1a, b). The reserves are located on the northern slopes of the 'Veľká Fatra' Mts. (NR Harmanecká tisina), 'Starohorské vrchy' Mts. (NR Pavelcovo) and 'Zvolenská kotlina' (NR Plavno). The NRs are part of the remnants of the limestone beech forests (approximately 350 ha; source National Forest Centre in Zvolen), a rare habitat representing species-rich plant associations included in the EU Habitat Directive and Natura 2000. Yew typically occurs in the understory of this beech-dominated habitat. In the 19th century, yew occupied the area to such an extent that it gained economic significance, and the timber was exported to the entire Habsburg monarchy (Korpeľ 1981). Since then, yew occurrence has gradually decreased because of (i) intensive cutting practices (clear-cuts, large-scale shelter wood-cuts), (ii) increasing damage due to herbivory, and iii) continual harvesting of

Table 1 Description of the study sites

Site characteristics	NR Harmanecká tisina	NR Plavno	NR Pavelcovo
Latitude (°N)	48°50′00″	48°43′52″	48°46′22″
Longitude (°E)	19°01′02″	19°14′09″	19°07′26″
Altitude (m a.s.l.)	630–780	400–530	520–710
Area of nature reserve (ha)	20.04	28.08	28.65
Slope (°)	30–40	20–30	20–30
Bedrock		Dolimitic limestone	
Soil type		Cambic Rendzic Leptosols	
Permanent research plots			
Plot name	U	U/S/C	U/T
Number of plots	1	2/2/2	2/2
Plot size (ha)	0.5	0.30[a]	0.21
Number of tree species	6	6/6/8	10/10
Year of establishment	1995	1972	1989
Years of measurement	1995, 2005, 2016	1972, 1982, 1993, 2003, 2013	1989, 1999, 2004, 2016

NR nature reserve, *U* unmanaged plot, *T* plot with the combination of negative crown and moderate low thinning, executed in 1990 (intensity of 14% and 18% from the growing stock) and in 2000 (intensity of 11% and 12% from the growing stock), *S* plot with selective shelter wood-cut, all subcanopy trees removed except yew (in 1972, intensity of 29% and 27% from the growing stock, and in 1987, intensity of 8% and 7% from the growing stock), *C* plot with the incomplete small-scale clear-cut executed in 1972, all trees removed except yew

[a]The area of research plots C1 and C2 was 0.16 and 0.20 ha, respectively, whereas 0.30 ha was used for the other plots

yew timber (Barták 1929; Korpeľ 1981). As early as in the middle of the 20th century, the effort to conserve the most valuable yew populations led to the declaration of strict nature reserves NR Harmanecká tisina and NR Plavno. In this period, the locality Harmanec, which includes the NR Harmanecká tisina, was documented as the area with the largest scattered occurrence of yew in Europe [approximately 160,000 individuals on an area of 860 ha (Svoboda 1947) and 300,000 individuals including the regeneration on an area of 3000 ha (Tschermak 1949)]. By contrast, a considerable, concentrated occurrence of over 10,000 yew individuals (height over 1.3 m) was recorded in the NR Plavno on an area of only 27 ha (Korpeľ and Paule 1976); and later also in the protected area of Pavelcovo, declared a NR in 1998 (approximately 6000 individuals on an area of 5 ha). In the following period, despite the consistent application of the non-intervention principle in these NRs, yew continued to decline further. As a result, intensive research was initiated during the 1970s, focusing particularly on the conservation of the endangered tree species by silvicultural treatments (Korpeľ and Paule 1976; Korpeľ 1981). Additionally, several protective measures were also enacted (mesh tree guards and construction of fences, among others); however, often with only limited and short-term effects.

The study localities are affected by a moderately cold (NR Harmanecká tisina, with mean annual temperature of 5.0–5.5 °C) or a moderately warm climate (NRs Pavelcovo and Plavno, with mean annual temperature of 7.5–8.0 °C), with an average annual precipitation of 850–950 mm. Limestones and dolomites form the bedrock overlaid by a medium depth rendzina (Saniga 1996, 2000). European beech (*Fagus sylvatica*) and yew

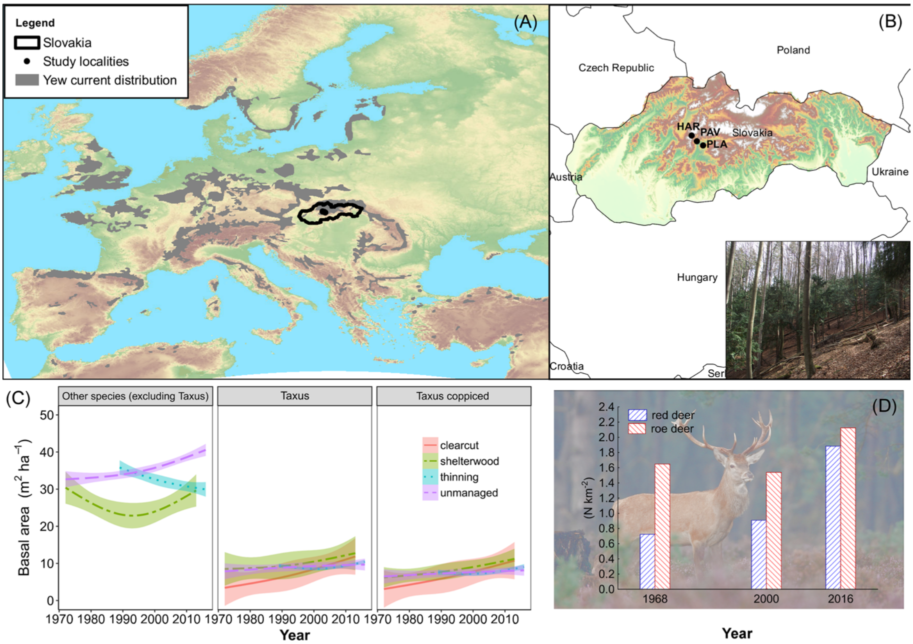

Fig. 1 **a** Current distribution of European yew (EUFORGEN 2016) overlaid with representation of terrain surface (1 × 1 km resolution; dark brown—high mountains, green—lowland); **b** Geographical location of the study sites with permanent research plots within Slovakia overlaid with digital terrain model (30 × 30 m resolution; white—high mountain peaks, light green—lowland); an example picture of the population of European yew in the study site NR Plavno (photo taken by J. Pittner in spring 2013); **c** development of the stand basal area of European yew and other tree species averaged by the management treatments during the period 1970–2016; **d** populations of red and roe deer in central Slovakia according to annual state-wide game census in 1968, 2000, and 2016 (data provided by National Forest Centre in Zvolen). (Color figure online)

as dominant species are often admixed with sycamore maple (*Acer pseudoplatanus*), Norway spruce (*Picea abies*), common ash (*Fraxinus excelsior*), and European larch (*Larix decidua*). Stands with a diverse vertical structure were established at the turn of the 19th and 20th century, after large-scale shelter wood-cuttings and clear-cuttings. These stands originated from irregular natural regeneration of yew, beech, maple, and fir trees supplemented by planting of spruce, larch, and pine. Yew regenerated either before the harvesting of the canopy stand or later in small gaps that occurred in the beech-dominated thickets of the new stands (Korpeľ and Paule 1976; Korpeľ 1996).

Experimental design and sampling

The experiment included eleven permanent experimental plots ranging in area from 0.16 to 0.50 ha. Six plots were normally managed by silvicultural treatments, whereas five were left unmanaged for use as control plots (Table 1). The silvicultural treatments included shelter wood, clear-cut, and thinning. Clear-cut and shelter wood-cut were applied in four of the six plots established in the NR Plavno in 1972 (Korpeľ and Paule 1976); thinnings were conducted in two of the four plots established in the NR Pavelcovo in 1989 (Korpeľ 1996). Size of all plots, but especially those managed, was strictly limited and the cuttings required a written permission of the State Nature Conservation Agency, the Ministry of Environment of the Slovak Republic. After the cuttings, all logs were removed from the plots. The plots were separated by 10–15 m-wide stripes that were left untouched. In the NR Harmanecká tisina, one unmanaged control plot was established in 1995 (Saniga 1996). In all experimental plots, repeated measurements were conducted at 5–12-year intervals (Korpeľ and Paule 1976; Korpeľ 1995, 1996; Saniga 1996, 2000). For all living trees that reached the diameter at breast height (DBH) > 2 cm, we recorded tree species and DBH. Stem damage was additionally assessed for the yew trees. For more detailed measurements of trees with DBH ≤ 2 cm (regeneration), a 10 × 40–70 m (400–700 m^2) transect was placed at the centre of each plot. In transects, the trees were classified into the following height classes: < 10, 10–20, 21–50, 51–130 and >130 cm (up to DBH of 2 cm). Hereafter, individuals of the first height class (< 10 cm) are called seedlings and those with the height > 10 cm saplings. In 2017, damage by deer browsing was additionally assessed as the percentage of the heavily (repeated browsing of the terminal shoot and a significant loss of lateral shoots) or moderately (preserved terminal shoot, negligible loss of lateral branches) damaged yew trees in regeneration on all plots.

Derivation of stand characteristics

Stand basal area per hectare (G_{ha}, $m^2\ ha^{-1}$) and number of trees per hectare with DBH above 2 cm (N_{ha}, trees ha^{-1}) were calculated from individual tree data for each inventory since plot establishment. Three alternatives of G_{ha} were computed: (a) of yew trees only, (b) of all tree species including yew (thereafter as Gha stand), and (c) of all tree species excluding yew. Number of yew trees per hectare was calculated in two ways: (a) each monocormic (one main trunk without ramification) or polycormic yew (2 and more trunks ramified immediately above the ground) was considered one individual, or (b) each trunk of a monocormic or polycormic yew was treated as an individual. The results of the two approaches were then displayed and compared. This approach was taken to allow for further comparisons with various studies related to European yew across the species distribution. We further calculated the relative stand density (RSD) as the ratio of the stand basal area to an average stand basal area of the stands at the same age. RSD was used to remove the effect of age (time) on the stand basal area and to distinguish between low-density and high-density stands compared with the average-density stands of the sample.

The Gini coefficient (Gini 1912) was used to characterise tree DBH inequality. This index was preferred over other commonly used indices, e.g., Shannon entropy index, because the index better characterises asymmetric competition between trees (Cordonnier and Kunstler 2015) and better discriminates between stands of different diameter distribution (Valbuena et al. 2012). The Gini coefficient index ranges from 0 (perfect equality, where all values are the same) to 1 (maximum theoretical inequality).

We used the Shannon diversity index (also known as Shannon–Weaver diversity index or Shannon entropy, Shannon 1948) to characterise tree species diversity of the stand (canopy trees) and the regeneration layer. This commonly used diversity index (Grossiord et al. 2014) was preferred over other indices (Purvis and Hector 2000) because it accounts for both species richness and species evenness. The index quantifies the uncertainty in predicting the species identity of an individual who is sampled at random from an infinitely large community. When the uncertainty is high, the diversity of the community is high.

Statistical analyses

We used Pearson's correlation to quantify associations between the stand and regeneration characteristics (Fig. S1), and correlations significant at the 95% confidence level were identified. We further used AIC in a stepwise algorithm (both directions) to identify explanatory variables that significantly contributed to explaining the variability in the abundance of yew regeneration. In the next, we applied a linear mixed-effects modelling technique (ME, Laird and Ware 1982) to quantify the effect of the selected variables on yew regeneration. ME was preferred over fixed-effects models because our sample design included long-term repeated measurements (Wallace and Green 2002), and the technique accounts for between-plot and between-site differences driven by factors not considered by the study. In the ME, the explanatory variables were set as fixed factors, whereas the year and the plot identity were used as random factors to account for repeated-measures design. Intercept and slope of the models were both fixed and random, and their variance was estimated. Since the effects of explanatory variables differed between the plots, we used the slope of the function nested to plot as a random factor. First, we fitted a base model that included only the effect of time. In the next step, the other variables (identified by stepwise regression to have a significant contribution) were added to the base model, and ANOVA using a likelihood ratio test was applied to test whether the additional variables significantly contributed to the explanation of the variability in yew abundance. For ANOVA, because the compared models differed in the number of fixed effects, we fitted the models by maximising log-likelihood (ML). However, the restricted maximum likelihood method (REML) was preferred to develop the final model because ML is biased for the estimation of variance components (Patterson and Thompson 1971). The package "nlme" (Pinheiro et al. 2014) was used for fitting the models. All analyses for the study were performed in R software (R Core Team 2017).

Results

Factors affecting yew regeneration

In general, G_{ha} increased over the study period (Fig. 1c), whereas the number of trees decreased (Fig. S2). The pattern of G_{ha}, however, varied among the plots due to different silvicultural treatments applied and different natural mortality occurred. The basal area of yew trees continually increased in all plots, whereas the change differed between the treatments for other species.

Correlation analysis identified species diversity of both the regeneration (Hreg, $r = 0.62$, $p < 0.01$) and the canopy layer (Hstand, $r = 0.37$, $p < 0.05$) to have significant positive correlation with the yew regeneration abundance (Fig. S1). Moreover, the diversity of the canopy layer correlated significantly with the diversity in regeneration ($r = 0.39$, $p < 0.05$). The stand characteristics such as stand G_{ha} (Gha_stand), relative stand density (RSD) and tree size structure expressed by Gini coefficient (gini) did not exhibit significant correlations with yew regeneration (all correlations had $p > 0.05$). However, the RSD and Gha_stand showed significant relationships with the proportion of yew individuals in the regeneration ($r = 0.42$, $p < 0.05$ and $r = 0.35$, $p < 0.05$, respectively).

Using the ME, we revealed that the abundance of the yew recruitment did not change significantly over the time but positively correlated with the tree species diversity of the regeneration (an increase of seedling abundance by 1650 ± 370 per increase of diversity index by 1; Table 2, Fig. 2). Further inclusion of stand variables such as species diversity of the canopy layer (Hstand), RSD, basal area of yew canopy trees (Gha_taxus), proportion of yew from stand basal area (taxus_prop) and proportion of beech from stand basal area (beech_prop) did not significantly contribute to the explanation of the variability (Table S1). Over the study period, changes in forest stand density (Fig. S2) and tree species diversity (Figs. S3, S4) differed among the sites and plots (Fig. 3). High tree species diversity (Shannon index > 1.5) showed positive relationship with the establishment of yew regeneration. However, a high dominance of beech trees in the regeneration layer was related to the reduced yew establishment and survival, whereas an increased proportion of maple trees showed a positive correlation (Fig. 4).

Effect of forest management on yew establishment

Concerning the management treatments, the relationship between species diversity and yew regeneration was strongest in the thinning variant, whereas the effect of no-management and clear-cut on the relationship was limited. The weakest correlation was found in Harmanec and Plavno, which are the sites with the overall lowest species diversity of all sample plots (Shannon index < 1.5). The largest variability in the regeneration quantity was found in the unmanaged stands (Figs. 2, 3). In general, the regeneration was weakest in the no-management variant, with the exception of the stands at the Pavelcovo site, where the high mortality rate of mature yew trees occurred during the study period (Fig. S2).

The density of yew regeneration decreased over time (Fig. 3). The exception was an increased density in the Pavelcovo locality, irrespective of the management type applied. High mortality of the mature yew trees in these plots (Fig. S2) and an increase in the tree species diversity of the regeneration layer (Fig. S3) coincided with the observed abundance of yew regeneration. The high regeneration intensity (Fig. 5) and the high tree species diversity (Fig. S4) found at the last measurement correlated with the abundant yew regeneration on the Pavelcovo locality.

Results of an assessment performed on the research plots in 2017 showed that deer game heavily damaged nearly 94% of the yew saplings.

Table 2 Result of the mixed-effects model applied to test the relationship of species diversity of regeneration (Hreg) and the abundance of yew regeneration

Effect	Fixed effects					Random effects	Goodness-of-fit statistics			
	Value	SE	df	t-value	*p* value	SD	AIC	BIC	R^2	RMSE
Intercept	2771.71	22,129.17	30	0.125	0.9012	397.86	613.68	624.57	0.46	944.13
Year	−2.02	11.07	30	−0.182	0.8566	0.26				
Hreg	1647.59	377.15	30	4.369	0.0001					

SE standard error, *df* degrees of freedom, *SD* standard deviation, *AIC* Akaike information criterion, *BIC* Bayesian information criterion, R^2 coefficient of determination, *RMSE* residual mean square error

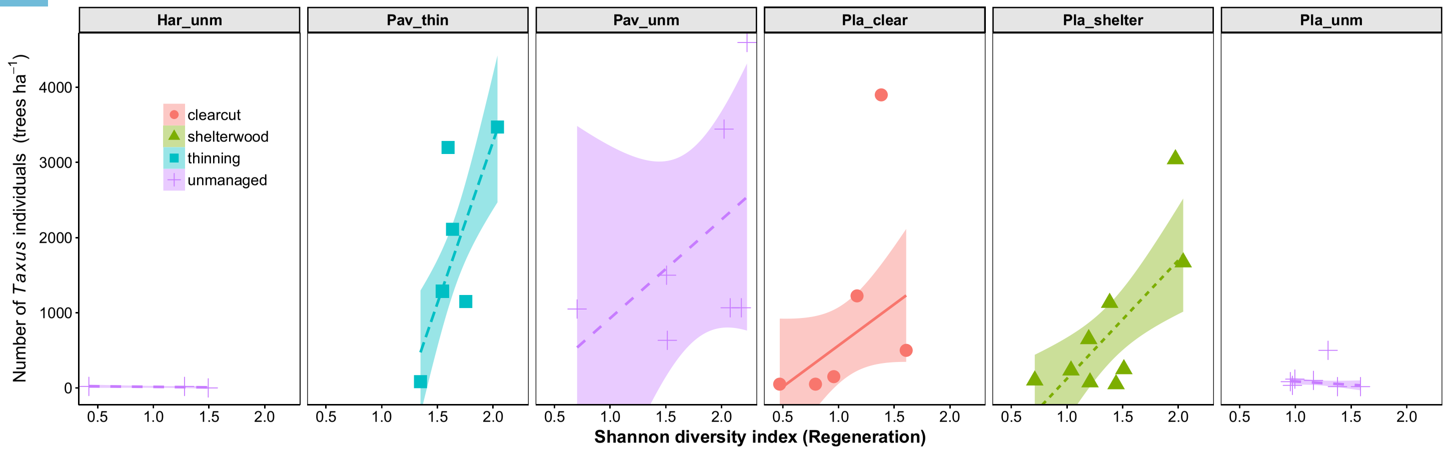

Fig. 2 Relationship of Shannon diversity index and yew regeneration (number of seedlings and saplings) at the sample localities (*Har* Harmanec, *Pav* Pavelcovo, *Pla* Plavno) and under different management treatments (*unm* unmanaged, *thin* thinning, *clear* clear-cut, *shelter* shelter wood)

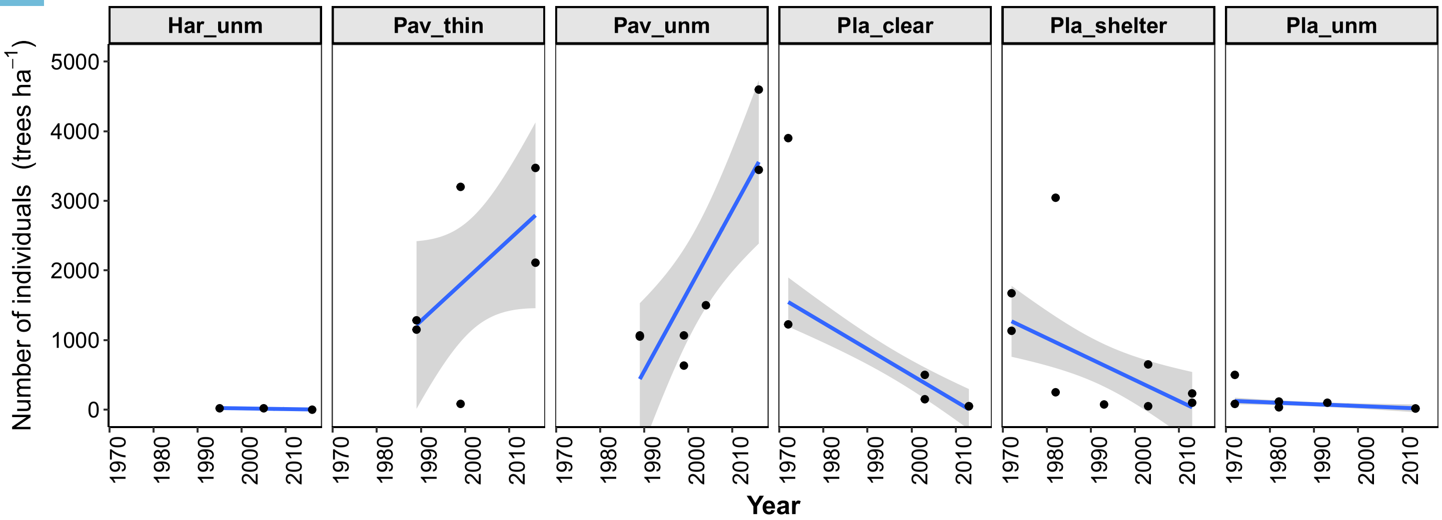

Fig. 3 Change in the yew regeneration over the study period at the sample localities (*Har* Harmanec, *Pav* Pavelcovo, *Pla* Plavno) and under different management treatments (*unm* unmanaged, *thin* thinning, *clear* clear-cut, *shelter* shelter wood)

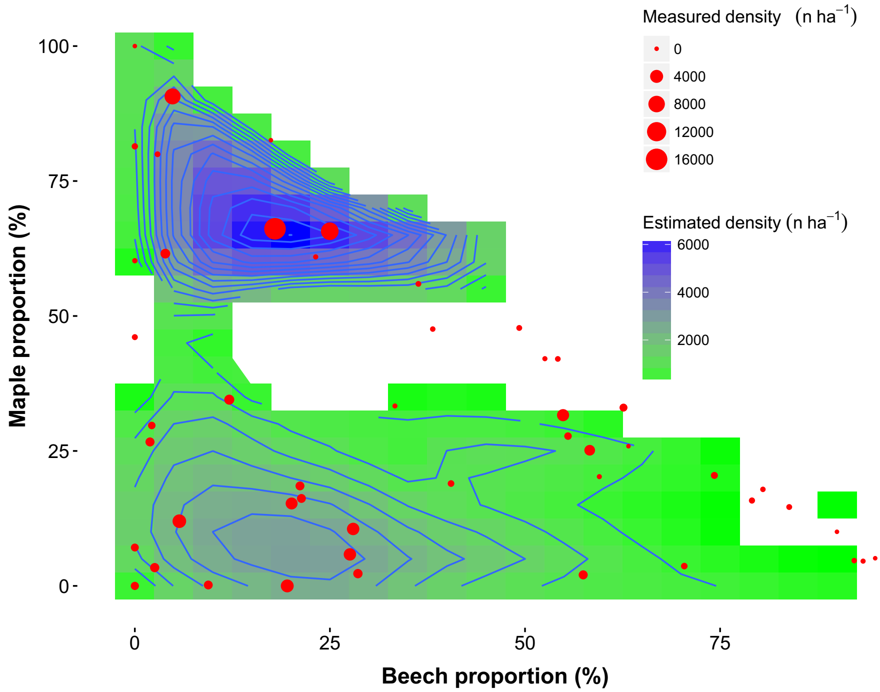

Fig. 4 Relationship of the proportions of beech and maple in the regeneration layer on the abundance of yew seedlings. To estimate the yew abundance at different combinations of beech and maple proportions, local polynomial regression was applied. We used the span parameter $\alpha = 0.4$ to control the degree of smoothing

Discussion

Effect of species diversity on yew establishment

Using the long-term observations, for the first time, we confirmed the positive correlation between species diversity and yew regeneration (H1). Although we revealed correlation, not cause-and-effect relationships, the possible beneficial effect of species richness can be explained by reduction in competition or facilitation, commonly called complementarity (Vandermeer 1989; Forrester and Bauhus 2016). In diverse forests in which tree species have contrasting functional traits, limited resources can be better distributed among the species (Tilman et al. 1997, 2001; Loreau et al. 2001). By contrast, functional niche overlap of admixed species may lead to an increase in competitive pressure (Rosenfeld 2002). The complementarity processes that drive diversity-recruitment relationships can be modified by various factors such as resource availability, or climatic conditions (Forrester and Bauhus 2016).

Early stages of seed germination and the further seedling growth are controlled primarily by seedbed properties (e.g., temperature, soil moisture and thickness; Suszka 1985). Therefore, seedlings can practically emerge irrespective of light intensity. The supply of light becomes important later, because subsequent successful establishment and survival of seedlings requires small canopy openings as more light-demanding herbs and seedlings of

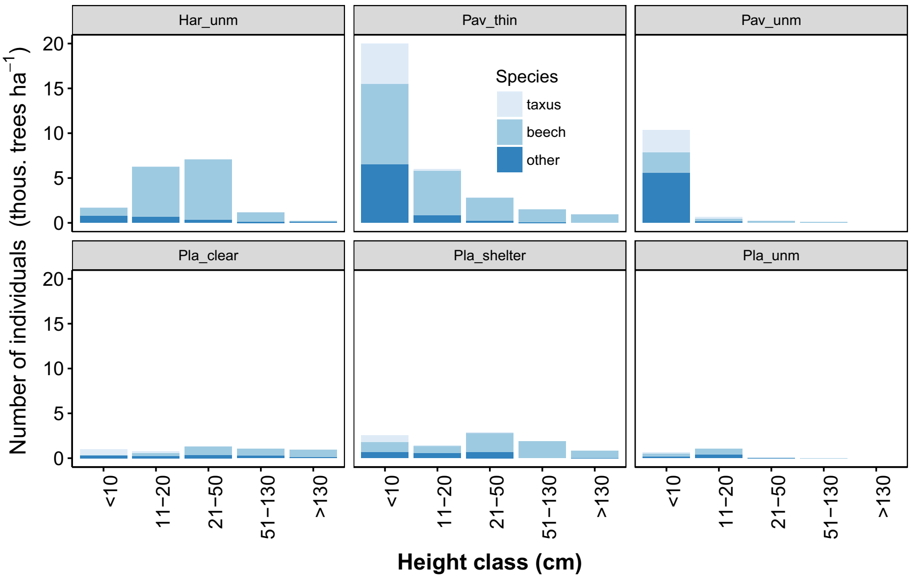

Fig. 5 Regeneration abundance of yew, beech and other tree species in height categories at the sample localities (*Har* Harmanec, *Pav* Pavelcovo, *Pla* Plavno) and under different management treatments (unm, unmanaged; thin, thinning; clear, clear-cut; shelter, shelter wood). Bars represent an average abundance over the study period. Yew (19%), beech (36%), maple (31%) and ash (6%) represent 92% of totally regenerated tree species individuals

broadleaved trees can have competitive advantage over yew seedlings at higher light levels (Iszkulo and Boratynski 2006). In our study, the regeneration abundance of yew, beech and other tree species was higher in the managed plots, most likely because of better light availability, than in the unmanaged plots (Fig. 5). However, higher variability among the plots related to site-specific factors and no replication for the management treatments did not allow us to make generalised conclusions.

In the first years after the establishment, the mortality rate of yew seedlings can be high due to limited light availability [i.e. less than 2–3% PPFD as described in Iszkuło and Boratyński (Iszkulo and Boratynski 2005)] and the stress from extreme low winter temperature events. In permanently low light conditions (which is characteristic for understory of the investigated beech stands; see also Kýpeťová and Jaloviar 2016), newly established yew seedlings competing with their neighbours for light invest minimal carbon resources to roots during the initial phase of the growing season (Iszkuło 2010). Natural regeneration in beech-dominated stands is usually very dense, where the belowground competition might become size-asymmetric (Schwinning and Weiner 1998), which additionally disadvantages yew seedlings and leads to their increased mortality rate. A possible shift in biomass partitioning, and a subsequent increase in the aboveground production at the expense of the belowground may explain high sensitivity of yew seedlings to abiotic stress factors. As suggested by Iszkuło (2010) or Iszkuło and Boratyński (2005), low light levels (below 2–7% PPFD) do not allow the seedlings to store a sufficient amount of assimilates, resulting in a decreased ability to overcome the low temperatures.

In our study, we found positive correlation between the proportion of maple in the regeneration (at the expense of beech) and the quantity of yew seedlings (Fig. 4). On the one hand, a higher proportion of maple regeneration might indicate better light availability that, at the same time, supports yew seedlings to survive and grow. In mixed-species forests, however, relatively high rates of soil nutrient mineralisation and high litter production and decomposition, resulting in elevated nutrient availability, significantly contribute to the facilitation effect (Boerner and Koslowsky 1989; Richards et al. 2010; Forrester and Bauhus 2016). Therefore, the increased proportion of maple might have facilitated yew regeneration because its leaves, in contrast to those of beech, have higher decomposition rates and are richer in nutrients (Boerner and Koslowsky 1989; Leuschner and Ellenberg 2017).

Overstory and yew seedlings

The highest correlation was found between the species diversity in the regeneration (Hreg) and the abundance of yew regeneration. Furthermore, the species diversity of the stand (Hstand) had a positive relationship with yew regeneration, but the effect was less consistent between the treatments. The less consistent relationship between the overstory and yew regeneration found in our study might be partly explained by a relatively stochastic regeneration process and factors not considered in our study. Limited size of experimental plots together with the possible influence of the neighbouring unmanaged forest stands, especially on the managed plots, might also have contributed to the weak relationship. Moreover, the effect was likely indirect, i.e., the high diversity of the canopy increased the diversity in the regeneration, which then positively affected yew regeneration (Fig. S1). In fact, species diversity of the canopy is consistently higher than diversity in the regeneration (Fig. S3 and S4). An intensive deer browsing most likely has caused the decrease in the number of regenerated species and significantly contributed to the dominance of beech in the height class above 50 cm (Fig. 5). Thus, the browsing attack likely appears not to be the factor that increases tree-species diversity (Schulze et al. 2014). This finding, however, contrasts to the Janzen-Connell hypothesis (Janzen 1970; Connell 1971).

The positive relationship between the high tree species diversity of canopy trees and regeneration is consistent with the previous findings by Liang et al. (2007) and Young et al. (2011). Yew regeneration can indeed benefit when growing under a tree species that is less shade tolerant than beech. A study from Poland showed that although yew seeds germinated under all canopy tree species, many seedlings were registered under broadleaved trees and most of the tree-like individuals under lime and hornbeam canopy trees (Iszkuło and Boratyński 2004).

Another factor reducing competition of understory yew trees for light is the difference in phenological phases of co-existing tree species. Yew recruitment and adults can benefit from being admixed with species that start a phenological phase later or end it earlier. Maple, lime and particularly ash have a shorter duration of the vegetative period than that of beech (Schieber et al. 2009; Vitasse et al. 2009), which partly explained the positive effect of the increased maple proportion at the expense of beech found in our study.

Other factors that likely drive diversity-recruitment relationships are stand density and tree-size structure. In our study, an increased RSD and stand basal area (G_{ha}) showed a positive correlation with the proportion of yew in the regeneration (Fig. S1). For successful yew regeneration, seedlings require a minimum of light and can grow below 5% RPPFD (Relative Photosynthetic Photon Flux Density, Perrin and Mitchell 2013). High shade tolerance and low susceptibility to diseases and pests may provide seedlings with an advantage in competition. Our results showed that yew recruitment was unaffected by tree-size diversity.

Conspecific mother trees can have a strong negative effect on germination and survival of yew seedlings (Dovčiak 2002; Thomas and Polwart 2003; Devaney et al. 2018). However, our results contrast with the above-mentioned studies as well as with the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). We provide no evidence for the negative effects of conspecific adults on the abundance of yew regeneration (Gha_taxus and taxus_prop in Table S1). Nevertheless, tree-level data including the coordinates of tree position in the stand (to allow for more detailed neighbourhood analyses, distance from conspecific adults or data on survivorship of yew seedlings) would be needed to properly test the Janzen-Connell hypothesis. It is also very likely that stronger negative interactions can occur in later life stages, after transition from seedlings to height classes of > 10 cm (Yan et al. 2015). The lack of saplings and missing single tree data, however, does not allow further testing.

The yew seedlings at the early stage of development often aggregate around the parent trees and experience higher mortality rates compared to areas beneath heterospecific adults, partly because of inhibition effects of the parent trees most likely related to substances in yew needles (García and Obeso 2003; Devaney et al. 2018) and easy access to herbivores. However, a sharp increase in the density of yew regeneration and a large decrease in the abundance of canopy yew trees found in the Pavelcovo locality indicated negative intraspecific relationships (Figs. 3, S2). Decline of the adult yew trees most likely resulted from a small-scale disturbance in 1993 (based on records provided by the forest enterprise). The reduced abundance of yew regeneration found in the plots after the clear-cut could be associated with more adverse microclimatic conditions for seedling germination. Furthermore, a trade-off between seedling low-light survival and high-light relative growth rate differs among tree species at various levels of canopy cover (Seiwa 2007). Open canopy conditions could be less favourable for yew growth compared with that of other tree species because yew loses indirect facilitation of adult trees. For yew, as a shade-tolerant tree species, the competition with canopy trees for light is less negative (unless it drops down below 2–3% PPFD) than the sudden increase in water and nutrient availability after a clear-cut and subsequent competition with vegetation mostly for water and nutrients available in the soil. Our results suggest that clear-cutting supported less yew regeneration than that of thinning. The area of clear-cut used in our study was relatively small (0.16–0.20 ha), but the rapid opening of the canopy supported development of beech regeneration that became too dense for other species to establish. Similar trend was also recorded in the variant of shelterwood cut (Figs. 3, S5). No replication for the management treatments, however, limits the results to be generalised. Nevertheless, management treatments can affect the species diversity of the regeneration by modifying the light intensity. However, such treatments can have only temporal effects, as recently discovered for beech-dominated forests in central Europe (Barna and Bosela 2015).

Yew saplings and adults

A continuous recruitment from seedling stage to saplings and young trees is crucial for conservation of yew (García et al. 2000; Mysterud and Østbye 2004). Indeed, the failure to survive was reported for many European yew populations (Hulme 1996; Dhar et al. 2007). Similarly, in our study, the regenerated yew failed to grow taller than 20 cm since 1982 (Fig. 5, Fig. S6). Most likely, the primary reason was the browsing by deer. Additional investigations performed by visual assessment on all research plots in 2017 showed that nearly 94% of the yew saplings were heavily damaged. The long-term absence of yew saplings in the height category 20–50 cm on all research plots can be explained by the increasing pressure of ungulates. Within the period of 1968–2016, the red and roe deer populations in the study region increased by 153% and 25%, respectively (Fig. 1d, Fig. S6). In several studies, a strong negative effect of browsing on yew recruitment was confirmed especially in the localities with high density of ungulates (Perrin et al. 2006; Dhar et al. 2007; Farris and Filigheddu 2008). Heavy pressure of ungulates in our research sites was indicated also indirectly by the absence of the tree species susceptible to browsing (maple, ash) in the height categories > 50 cm (Fig. 5). However, other factors, e.g. competition pressure from beech, could have also contributed significantly to the absence of these species.

The increased proportion of maple in the regeneration significantly correlated with the increased density of yew recruitment. The higher attractiveness of maple for deer browsers compared to beech can provide an explanation. Supporting mixed-species regeneration can therefore help to mitigate the selective browsing pressure (Gill 1992). This hypothesis can thus explain the beneficial effect of higher regeneration diversity on yew survival. Moreover, an admixture of other tree species (e.g. maple) in the regeneration provides a mechanical barrier against browsing of yew saplings (García and Obeso 2003).

In beech-dominated forests with dense beech regeneration, the conditions for yew establishment and growth are unfavourable (Svenning and Magård 1999). Because light requirements of yew saplings increase with age, their successful recruitment into the higher tree layers (ingrowth and recruitment) can be managed by silvicultural treatments (Köpp and Chung 1997). However, because of the heavy damage by deer browsing, we could not test the effects of different management and species diversity on the further growth of saplings. In our sites, browsing was found to have a significantly negative impact on the growth rate and needle morphology of yew saplings (Kýpeťová et al. 2018). As reported in other studies, in case of low density of ungulate population or when protected against browsing, yew saplings successfully recruit into the higher tree layers (Iszkuło and Boratyński 2005; Iszkuło et al. 2005; Devaney et al. 2018). In a recent study from a managed forest stand, close to one of our long-term plots in the NR Pavelcovo, the fencing and moderate silvicultural interventions were found to support ingrowth and recruitment of yew saplings (Kýpeťová and Jaloviar 2016). Persistent game management and/or consistent measures to protect yew trees (fencing, etc.) will need to be carried out to ensure conservation of yew in the study region to the future.

Transition from an abandoned open landscape and degraded forests towards dense beech-dominated forests has had a negative impact on the yew populations in Slovakia. In general, the strategy to conserve yew by a no-management approach (nature reserves) leads to ageing and decline of its population density (Korpeľ 1995). Our experiment aimed to explore long-term effects of different management alternatives on the development of yew populations. A reduced canopy cover positively influences the vitality, stability, and seed production (Saniga 2000), and as revealed in our study, the growth of the dominant yew trees. However, compared with the stands that were left to self-development, managed forests showed higher overall mortality of yew adults, particularly the suppressed ones (Fig. S2). Nevertheless, the reduced canopy closure which most likely stimulated the seed production could help the yew regenerate. The positive effects of the moderate cutting (improved light conditions, increased fructification, enhanced diameter increment, etc.) were reported to persist for 7–8 years at the most, especially limited by the strong lateral growth of beech crowns (Sedmáková et al. 2017). The above-mentioned observations and the results of our study allow us to conclude that the moderate thinnings with intensity not exceeding 20% of the growing stock applied every 5 years is likely an reasonable alternative to improve the status of yew populations. Because the increase in beech dominance reduced the species diversity (Fig. S4), management treatments should aim to support other tree species at the expense of beech and thereby help the yew to establish and develop. Suitability of clear-cutting is questionable and its application is limited because of the negative effect of the rapid reduction of the canopy cover on the viability and vitality of yew trees (Köpp and Chung 1997).

Conclusions

Our results suggested that tree species diversity, especially in the regeneration layer, positively correlated with abundance of yew regeneration. A small but positive correlation was found for species diversity in the upper canopy.

Current tree species composition of the forest stands in which European yew populations occur is sufficiently favourable for the regeneration of yew. To sustain or even improve regeneration, growth and vitality of yew trees, a selective cutting aimed at supporting increased species diversity is required. Extremely high population levels of deer most likely reduce the possible facilitation effects of tree species diversity.

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