

## RESEARCH ARTICLE

# Conservation and Sustainable Use of Forest Genetic Resources of English Yew (*Taxus baccata* L.) in Bavaria

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## ARTICLE INFO

**Article History**

Received: 09.09.2022

Accepted: 27.09.2022

First Published: 28.09.2022

**Keywords**

Genetic diversity

FGR

GCU

Conservation strategies

Seed stands

Isoenzyme markers



## ABSTRACT

For sustainable forest development a stable, functional, and therefore species-rich ecosystem is required to fulfil the diverse functions of forests. Rare tree species contribute substantially to diversity and provided an important habitat function for other species. Further, they have a vital impact on the stability of forest ecosystems and increase their biodiversity. Under climate change, these tree species become more important and should be planted in the forest to divide upcoming risks among different tree species. In the study altogether 906 trees from 19 populations of English yew were sampled evenly along the Bavarian distribution range. Our study based on 13 isoenzyme markers identified substantial genetic variation between the populations. Based on genetic variation within and between studied populations seed stands and gene conservation units (GCU) were proposed. In addition, following our results provenance recommendations were drawn. Selected forest genetic resources (FGR) will be presented in the Bavarian Forest reproductive material (FRM) information system. In addition to dynamic *in-situ* conservation, an *ex-situ* conservation of the English yew is sought through long-term seed storage and the establishment of a seed orchard. Thus, the first 19 plus trees have been selected. The number of plus trees should be increased by further selection taking into consideration the balance between female and male English yew trees. All efforts will have a strong impact on the conservation of the FGR of English yew in Bavaria.

**Please cite this paper as follows:**

Šeho, M., Fussi, B., Rau, B., & Kavaliauskas, D. (2022). Conservation and sustainable use of forest genetic resources of English yew (*Taxus baccata* L.) in Bavaria. *SilvaWorld*, 1(1), 52-67. <https://doi.org/10.29329/silva.2022.462.06>

**Introduction**

Forest genetic resources (FGR), defined as the sum of the genetic variation within tree species, represent an intergenerational value of social, economic, and ecological importance. Forest trees are defined as the keystone species of forest ecosystems. For many floral and faunal associations of the ecosystems is the continued existence of forests essential (Rajora & Mosseler, 2001). Increasing severe drought, pests and disease outbreaks, and stochastic events pose a major challenge for European forests and the forest sector under climate change conditions (Aitken et al., 2008; Lindner et al., 2010; Alfaro et al., 2014; Schelhaas et al., 2015). The possibility of long-lived forest trees surviving such changes in

a spatio-temporal heterogeneous environment depends on their adaptation capacities and genetic diversity. In the future with rapid environmental changes only high genetic variation will allow a population to respond and survive (Frankham et al., 2002; Willi et al., 2006). Therefore, initiatives to protect and conserve forest trees and their populations must ultimately aim at conserving intraspecific genetic diversity and genetic analyses within species at global and local scales are the basis for sustainable preservation of forest tree resources (Geburek, 1997; Fady et al., 2016). In addition to genetic diversity within populations, the preservation of regional differentiation and site-specific adaptation is an important goal (Donath & Eckstein, 2008).

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In the last few decades genetic conservation activities of FGR are increasing in Germany (Paul et al., 2010). To implement international and national strategies and requirements, Bavarian Office for Forest Genetics (AWG) developed a “Concept for the conservation and the Sustainable Use of Forest Genetic Resources in Bavaria” (Konnert et al., 2015). The concept serves as a basis for the long-term conservation of the genetic diversity and FGR of main, rare, and endangered trees and shrubs. The concept envisages actual conservation measures on a genetic basis. Collected detailed knowledge is an important step for deriving provenance recommendations, the identification of seed stands and for regionally typical conservation of genetic structures.

In contrast to the main tree species, for which numerous studies have already been carried out at AWG (Konnert & Cremer, 2011; Konnert et al., 2014; Neophytou et al., 2017; Fussi & Hübner, 2018; Šeho et al., 2022), there is a lack of knowledge for rare tree species like English yew in Bavaria for successful implementation of gene conservation measures. In Bavaria, 18 tree or woody species (excluding willow species) are currently assigned to the group of rare tree species (Schröder et al., 2013). They cover less than 2% of the Bavarian Forest area. Ten tree species mapped in the federal project account for less than 0.4% of the Bavarian Forest area (Riederer & Fritsch, 2013; Schröder et al., 2013; Huber et al., 2015). Most rare tree species like English yew are often fragmented and have small population sizes (Suppl. Figure 1). Isolation is thought to often disrupt gene flow between populations. In addition, genetic drift and bottleneck effects occur in small populations, which also lead to random gene losses in the short term and can further reduce the adaptability of the populations (Savolainen, 2000; Pardo et al., 2005).

The English yew occurs in Europe from Spain in the west to north Iran on the Caspian Sea. The northern limit of its distribution is in southern Norway and Sweden. In the South, it still occurs in the Atlas Mountains, Apennines, and Greece. Other occurrences are in the British Isles, Corsica, Sardinia, Sicily, and Gotland (Suppl. Figure 1). Mayol et al. (2015) found evidence that yew colonized Europe from the East, and that European populations separated into two groups (Western, Eastern) at the beginning of the Quaternary glaciations. In several European countries, English yew (*Taxus baccata* L.) is an endangered rare tree species (González-Martínez et al., 2010; Klumpp & Dhar, 2011; Linares, 2013; Litkowiec et al., 2018; Komárková et al., 2022). The English yew is one of Bavaria's rare and ecologically valuable tree species.

In Bavaria, there are three main areas of the natural distribution of English yew: on the Franconian Jura and in the Upper Palatinate Jura, in the Bavarian Forest, in the Alps and in the foothills of the Alps (Figure 1). Occurrences outside of these regions are mostly plantations or overgrown garden forms. In the Bavarian Forest, the English yew can grow up to 1,100 meters over sea level and in the Bavarian Alps up to 1,330

meters (Schütt, 1995; Hageneder, 2007). Due to slow growth, it develops an extensive root system, reaches tree heights of over 20 meters, and can cope with various site conditions (Scheeder, 1994). English yew was strongly pushed back in the last 500 years and partly isolated and currently prefers calcareous soils (especially on tuff rock) with a good water supply (Alps, Jura). The fact that today's forest picture in Germany and the whole of Europe is different is mainly because of human activity (Ruprecht et al., 2010). Numerous influencing factors such as isolation, strong population fragmentation, germination inhibition, slow growth and browsing pose an additional threat to English yew populations (Chybicki & Oleksa, 2018). The low and medium forest-type management was reduced in favour of high-forest management on a per-plot basis. After clear-cutting and reforestation with mainly fast-growing tree species such as spruce and shorter rotation times, the English yew could no longer occur and lost more and more of its habitat. Also because of their slow growth and the lack of possible uses of the English yew wood, their forestry importance has almost disappeared (Küster, 1994). In addition to this supposedly low silvicultural importance, the toxicity of the English yew (all parts except for the aril and pollen) posed a great danger to the animals and carters. To avoid deadly poisoning from eating English yew trees, they were immediately removed and replaced by other tree species (Scheeder, 1994). Furthermore, the consequences of climate change are becoming clearer and increasing the risk of dying populations of native tree species like spruce, larch, pine, beech, sycamore, or ash in Germany. The increasing number of forest tree species, e.g., scattered broadleaves and conifers and the establishment of mixed forests can diminish and distribute the risks since different species have differing susceptibility to various stressors and disruptive factors (Rotach, 1999; Spiecker, 2006; Knoke et al., 2008; Bauhus et al., 2017; Wolff et al., 2021; etc.). The focus increase on rare native tree species such as white elm, field maple, service tree and English yew, which can be used as possible alternatives. A major challenge with these tree species is the seed supply with high-quality forest reproductive material. Since these rare tree species are not subject to the FoVG and mostly played a secondary role in silviculture, no suitable seed stands have been selected so far. The aim of the project “Conservation of forest genetic resources and elaboration of provenance-recommendations and improvement of the harvesting possibilities for the rare tree species field maple (*Acer campestre* L.), European white elm (*Ulmus laevis* Pall.), service tree (*Sorbus domestica* L.) and English yew (*Taxus baccata* L.) in Bavaria was to give the first insight of genetic variation”. The genetic diversity of conservation units and forest stands plays a crucial role and is the most important scale for the future adaptation and survival of tree species under changing environmental conditions.

Today's natural occurrence of English yew is limited to special and often extreme locations such as steep slopes, rocks,

and inaccessible forests where cultivation is not worthwhile. These areas often have a protected status (NSG, NP, NWR, etc.); English yew is an endangered species under special protection (red list species) under the Federal Species Protection Law (BartSchV). If genetic exchange through pollen or seeds is missing between these areas of occurrence of English yew through steppingstone populations, there is a risk of genetic impoverishment (isolation) of these occurrences, which requires more detailed consideration (Scheeder, 1994; Riederer & Fritsch, 2013). Effects of isolation, in particular for dioecious tree species such as English yew, can include a reduced fructification capacity or a reduced germination capacity of the seeds through increased inbreeding. The sustainable use and importance of rare native tree species like English yew to promote and expand the mixed forest and to improve biodiversity on all three levels (gene, species, and ecosystem) have been widely discussed (UN, 1992; Bollmann & Braunisch, 2013; Laikre et al., 2010).

There are several rare native tree species in Bavaria, such as field maple, white elm, service tree, English yew, or wild service tree, which are not listed in the EU directive 1999/105/EC (EU, 1999) and in the German Forest Reproductive Material Act (FoVG, 2003) and are not included in the EU list which is the basis for the production and marketing of FRM of important native and naturalized tree species. For these tree species, there are no legal requirements regarding the production and trade of FRM, endangering the regional gene pool and the future quality of the stands. At the same time, there are currently initiatives at the EU level to expand the above-mentioned Directive 1999/105/EC to include rare tree species like English yew.

To reach the aims of our study we used isozyme markers to estimate the genetic variability for 19 populations of English yew, and to investigate the partitioning of the genetic variation

among studied populations. Overall, isozymes had a long history in plant and forest genetic variability studies, to estimate the genetic diversity and populations structure within natural forest stands (Doligez & Joly, 1997; Ritland et al. 2005; Porth & El-Kassaby, 2014).

Therefore, the aims of our study were: (i) to analyze the genetic structure and diversity of English yew in Bavaria; (ii) to identify and propose new seed stands for English yew in Bavaria; and (iii) to discuss and select GCUs for English yew in Bavaria based on level of genetic variation; (iiii) to generate knowledge for sustainable use of English yew FRM; (iiiii) based on collected knowledge to enable *ex-situ* conservation measures.

## Materials and Methods

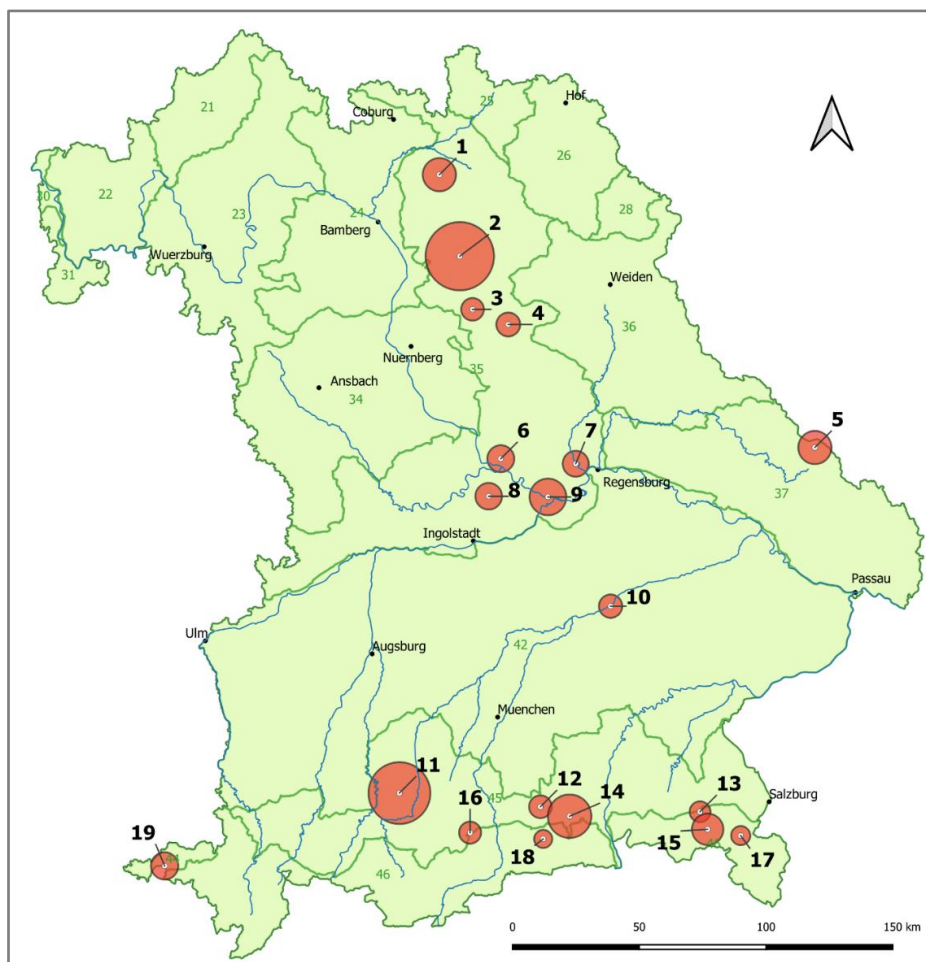
### English Yew Tree Stands Selection and Sampling

Material for this study was collected in the federal State of Bavaria, Germany in 2019. For the genetic characterization, it is intended to sample the Bavarian range of English yew as representatively as possible. The following stand selection criteria were used: minimum number of trees  $\geq 20$  trees; minimum diameter at breast height (DBH), which was a proxy for evaluation of fructification capacity; good stand health condition and stem quality; stand accessibility and possibility for seed collection; autochthonous stand or the origin of the stand should be known; distance from the nearest poor-quality population of more than 400 meters. In total 906 trees from 19 natural English yew tree populations distributed over Bavaria were sampled for genetic analysis (Table 1 and Figure 1). The sample size per population varied from 35 to 51 mature trees. Buds were sampled from mature male and female trees distanced at least 30-40 meters apart.

**Table 1.** Sampled English yew populations in Bavaria

| No. | Sample size | Location         | Stand area (ha) | No. of trees in the stand | m. a. s. l. | District       |
|-----|-------------|------------------|-----------------|---------------------------|-------------|----------------|
| 1   | 49          | Schammendorf     | 5.9             | 476                       | 400         | Lichtenfels    |
| 2   | 49          | Gößweinstein     | 32.0            | 2900                      | 440         | Forchheim      |
| 3   | 50          | Algersdorf       | 4.0             | 120                       | 500         | Lauf           |
| 4   | 50          | Schloß Neidstein | 3.6             | 150                       | 490         | Sulzb.-Rosenb. |
| 5   | 50          | Bayer. Wald      | 200.0           | 475                       | 680-1000    | Freyung-Graf.  |
| 6   | 50          | Neutal           | 12.6            | 240                       | 410         | Neumarkt       |
| 7   | 50          | Penk             | 1.3             | 210                       | 390         | Regensburg     |
| 8   | 50          | Zandt            | 3.2             | 230                       | 510         | Eichstätt      |
| 9   | 50          | Kelheim          | 112.0           | 630                       | 380         | Kelheim        |
| 10  | 39          | Landshut         | 18.5            | 137                       | 460         | Stadt Landshut |
| 11  | 51          | Paterzell        | 39.2            | 2320                      | 690         | Weil.-Schongau |
| 12  | 40          | Gotzing          | 1.7             | 122                       | 700         | Miesbach       |
| 13  | 50          | Siegsdorf        | 5.2             | 81                        | 750         | Traunstein     |
| 14  | 50          | Au               | 30.3            | 1000                      | 660         | Miesbach       |
| 15  | 50          | Ruhpolding       | 100.0           | 400                       | 920         | Traunstein     |
| 16  | 44          | Bichl            | 5.2             | 106                       | 620         | Bad Tölz       |
| 17  | 49          | Karlstein        | 3.0             | 50                        | 620         | Bercht. Land   |
| 18  | 35          | Tegernsee        | 1.6             | 35                        | 1100        | Miesbach       |
| 19  | 50          | Sigmarszell      | 8.5             | 250                       | 650         | Lindau         |

m. a. s. l.: meters above sea level, the codes in Table 1 correspond to the codes in the map in Figure 1 and Table 2.



**Figure 1.** Distribution of sampled populations of English yew in Bavaria (codes on the map correspond to the codes in Table 1). The size of the circle corresponds to actual population size.

### Genetic Analysis

For the genetic characterization of the English yew samples, isoenzyme analyzes (biochemical-genetic characterization) of 13 gene loci were applied according to Hertel (1996). The following enzyme systems or controlling gene loci were included in the analyzes: AAT-A, AAT-B (enzyme system: aspartate aminotransferase, E.C. 2.6.1.1), ADH-A (enzyme system: alcohol dehydrogenase, E.C. 1.1.1.1), IDH-A, IDH-B (enzyme system: isocitrate dehydrogenase, E.C. 1.1.1.42), LAP-A, LAP-B (enzyme system: leucine aminopeptidase, E.C. 3.4.11.1), MDH-C (enzyme system: malate dehydrogenase, E.C. 1.1.1.37), MNR-A (Enzyme system: menadione reductase, E.C. 1.6.99.2), 6-PGDH-A (Enzyme system: 6-phosphoglucose dehydrogenase, E.C. 1.1.1.44), PGI-B (Enzyme system: phosphoglucose isomerase, E.C. 5.3.1.9), PGM-A (enzyme system: phosphoglucose mutase, E.C. 2.7.5.1), SDH-B (enzyme system: shikimate dehydrogenase, E.C. 1.1.1.25). The isoenzyme analysis was performed using starch gel electrophoresis and procedures used by Hertel (1996).

### Data Analysis

Based on the multilocus genotypes determined for the individual trees, the allele frequencies, and the following parameters, which describe the genetic variation within the natural distribution, were first calculated [Software SAS, package MacGen (Stauber & Hertel, 1999)]:

- The allele frequencies at 13 gene loci in the 19 yew occurrences examined.
- $N_e$ : genetic diversity as the mean number of effective alleles per locus ( $N_e$ ) and as hypothetical gametic multilocus diversity ( $V_{gam}$ ).

The genetic differences between the populations were quantified by the genetic distance according to Gregorius (1974). Furthermore, the genetic differentiation between the populations was determined using the differentiation measure  $D_j$  according to Gregorius and Roberds (1986). These calculations are also based on the individual collectives' distribution of alleles as allele frequencies (Software SAS, package MacGen). Genetic diversity statistics (e.g., number of different alleles ( $N_a$ ), effective ( $N_e$ ) alleles ( $N_p$ ), observed ( $H_o$ )/expected ( $H_e$ ) heterozygosity) were calculated using



GenAlEx 6.5 (Peakall & Smouse, 2006, 2012) per loci and for each population. The Analysis of Molecular Variance (AMOVA) was performed using GenAlEx 6.5 (Peakall & Smouse, 2006, 2012) (for the significance test we used 9999 random permutations). The inbreeding coefficient ( $F_{IS}$ ) was assessed per locus and sample, as well as a test of whether it is significantly positive or negative (significant deficit or excess of heterozygotes, respectively) with Fstat 2.9.3. software (Goudet, 2001). Allelic richness ( $Ar$ ) was estimated with Fstat 2.9.3. software (Goudet, 2001), which estimates  $Ar$  per locus and sample, and overall samples based on the lowest number of samples (30 samples were used for rarefaction in our study).

### Genetic differentiation between English yew populations

The genetic structure and differentiation between English yew populations were estimated using several methods: (a) the Analysis of Molecular Variance (AMOVA) was performed using GenAlEx 6.5 (Peakall & Smouse, 2006, 2012) (for significance test it was used 9999 random permutations); (b) pairwise differentiation based on Nei (Nei, 1972) genetic distances between all pairs of populations (GenAlEx 6.5); (c) the Bayesian clustering approach as the model-based clustering algorithm implemented in STRUCTURE 2.3.3 software (Pritchard et al., 2000). The online software CLUMPAK was used for identifying clustering modes and packaging population structure inferences across K and visualizing the clustering (Kopelman et al., 2015).

## Results

### Allele Frequencies

In total 19 English yew populations (Figure 1) were sampled, and 906 trees were genotyped. A total of 41 gene variants (alleles) were detected based on 13 isoenzyme markers (Suppl. Table 1 shows the allele frequencies at 13 gene loci in the 19 English yew populations). Two of the 13 gene loci (AAT-A and MDH-C) were monomorphic.

### Genetic Diversity

Genetic variation parameters within populations are given in Table 2. The genetic diversity, i.e., the mean number of gene variants per gene locus, varies in the English yew populations between 2.15 (populations 6-Neutal, 14-Au, 15-Ruhpolding, 18-Tegernsee, 19-Sig-marszell) and 2.46 (populations 1-Schammendorf, 4-Neidstein Castle, 10-Landshut). The genetic diversity ( $V_{gam}$ ) varied substantially between 33.01 (in population 8-Zandt) and 773.65 (population 10-Landshut). The effective number of alleles ( $N_e$ ) varied between 1.36 (in population 8-Zandt) and 1.79 (population 10-Landshut). With a few exceptions, the  $F_{IS}$  values were close to zero. Only three populations show slightly higher positive values of inbreeding [ $F_{IS} = 0.087$  (populations 5-Bayerischer Wald, 9-Kelheim) and  $F_{IS} = 0.112$  (in population 10-Landshut)]. Thus, there are fewer heterozygous individuals in these populations than under the Hardy-Weinberg equilibrium would be expected. In contrast, population 3-Algersdorf had  $F_{IS} = -0.122$  which indicates an excess of heterozygous (Table 2 and Suppl. Figure 2).

**Table 2.** The within-population genetic diversity parameters based on isoenzyme analyzes at 13 gene loci

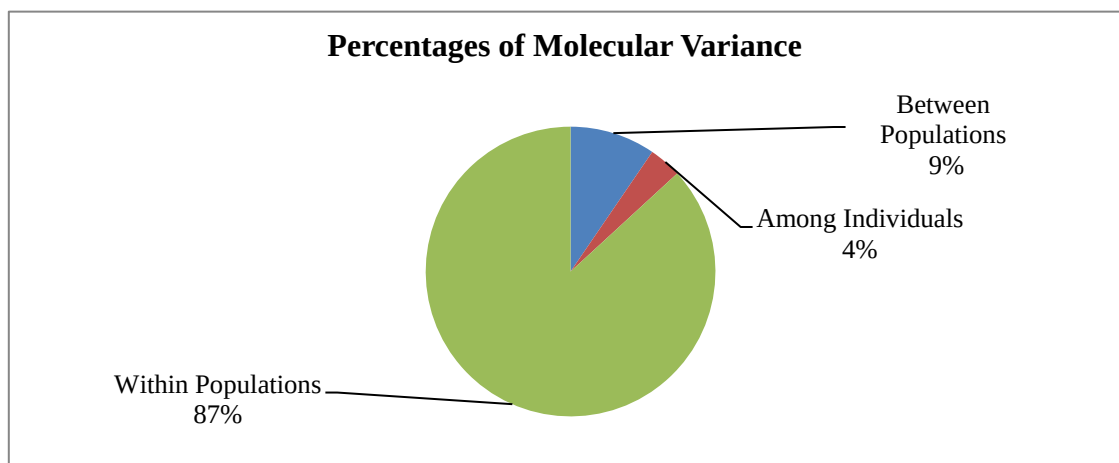
| Population        | Location         | Na   | Ne   | Ar   | Vgam   | Ho    | He    | $F_{IS}$ |
|-------------------|------------------|------|------|------|--------|-------|-------|----------|
| 1                 | Schammendorf     | 2.46 | 1.49 | 2.42 | 83.76  | 0.251 | 0.253 | 0.003    |
| 2                 | Gößweinstein     | 2.38 | 1.61 | 2.33 | 138.67 | 0.259 | 0.264 | 0.005    |
| 3                 | Algersdorf       | 2.23 | 1.58 | 2.17 | 176.00 | 0.331 | 0.290 | -0.122   |
| 4                 | Schloß Neidstein | 2.46 | 1.62 | 2.42 | 202.18 | 0.289 | 0.295 | 0.020    |
| 5                 | Bayerischer Wald | 2.23 | 1.64 | 2.22 | 290.30 | 0.306 | 0.317 | 0.087    |
| 6                 | Neutal           | 2.15 | 1.61 | 2.15 | 212.35 | 0.283 | 0.299 | 0.055    |
| 7                 | Penk             | 2.31 | 1.59 | 2.19 | 160.87 | 0.293 | 0.279 | -0.030   |
| 8                 | Zandt            | 2.23 | 1.36 | 2.11 | 33.01  | 0.228 | 0.209 | -0.073   |
| 9                 | Kelheim          | 2.23 | 1.56 | 2.21 | 155.05 | 0.261 | 0.285 | 0.087    |
| 10                | Landshut         | 2.46 | 1.79 | 2.44 | 773.65 | 0.347 | 0.361 | 0.112    |
| 11                | Paterzell        | 2.38 | 1.68 | 2.32 | 314.57 | 0.295 | 0.312 | 0.051    |
| 12                | Gotzing          | 2.23 | 1.57 | 2.21 | 201.11 | 0.306 | 0.305 | -0.020   |
| 13                | Siegsdorf        | 2.38 | 1.69 | 2.33 | 315.56 | 0.317 | 0.313 | -0.028   |
| 14                | Au               | 2.15 | 1.56 | 2.14 | 167.54 | 0.291 | 0.292 | -0.009   |
| 15                | Ruhpolding       | 2.15 | 1.59 | 2.11 | 166.85 | 0.289 | 0.284 | -0.027   |
| 16                | Bichl            | 2.38 | 1.76 | 2.37 | 569.30 | 0.327 | 0.342 | 0.020    |
| 17                | Karlstein        | 2.23 | 1.68 | 2.23 | 344.06 | 0.290 | 0.317 | 0.065    |
| 18                | Tegernsee        | 2.15 | 1.59 | 2.15 | 145.64 | 0.277 | 0.275 | -0.001   |
| 19                | Sigmarszell      | 2.15 | 1.58 | 2.15 | 212.20 | 0.294 | 0.304 | 0.037    |
| <b>Total mean</b> |                  | 2.28 | 1.61 | 2.24 | 245.40 | 0.291 | 0.295 | 0.012    |

N: Sample number, Na: Mean no. of different alleles, Ne: Mean no. of effective alleles, Ar: Mean allelic richness (based on minimum sample size of 30 diploid individuals.), Vgam: Hypothetical gametic multilocus diversity, Ho: Observed heterozygosity, He: Expected heterozygosity,  $F_{IS}$ : Inbreeding coefficient.

### Genetic Differentiation and Cluster Analysis

Figure 2 shows the hierarchical distribution of genetic variation at different levels (AMOVA). Most of the total

variation is split between populations (9%) and within populations (87%). The value of 9% is relatively high for a wind-pollinated tree species.

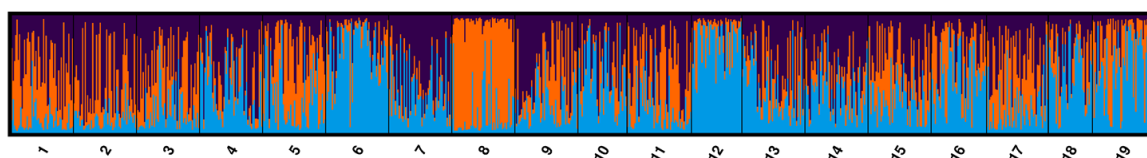


**Figure 2.** The distribution of genetic variation between and within populations based on the fixation index ( $F_{ST}$ ) [GeneAlex6.5 Software (Peakall & Smouse, 2006, 2012)].

According to a large number of sampled populations in a relatively small area, the value for the population differentiation based on  $F_{ST}$  can be rated as relatively high. Viewed from another perspective, a comparably high value would be expected for a small number of populations across Europe. The values  $\delta$  of the genetic distances (allelic) are given in Suppl. Table 2. Values  $\delta$  above 0.10 are to be rated as comparatively high and indicate high genetic differences between the populations. The highest distance was found between populations 1-Schammendorf and 12-Gotzing, and between 8-Zandt and 10-Landshut with 0.35. A distance of 0.34 is found between the populations 8-Zandt and 4-Schloss Neidstein, 7-Penk, 12-Gotzing, 14-Au. In contrast, the distance between the populations 11-Paterzell and 13-Siegsdorf, as well as between 9-Kelheim and 13-Siegsdorf is significantly smaller at only 0.12. The differentiation values of  $D_j$  shown in Suppl. Figure 3 quantify the difference in the allelic composition of each population compared to the allelic structure of the entire examined material. The mean differentiation ( $\delta$ ) is given overall nineteen populations. It is an indicator of the genetic

heterogeneity of the examined yew populations. The mean differentiation  $\delta$  is rated as high as 10%, whereby the stand 8-Zandt stands out with the highest differentiation value ( $D_j = 18.9\%$ ). This inventory is by far the least representative of the entire study material. The 11-Paterzell, 13-Siegsdorf and 17-Karlstein populations are the least differentiated and therefore the most representative of the overall gene pool. The combination of low differentiation and quite high diversity in these populations makes them very well suited for the conservation of this tree species together with populations from 10-Landshut and 16-Bichl with extremely high diversity. Pairwise Population Matrix of Nei (1972) genetic distance (Software GeneAlex6.5) is given in Suppl. Table 2.

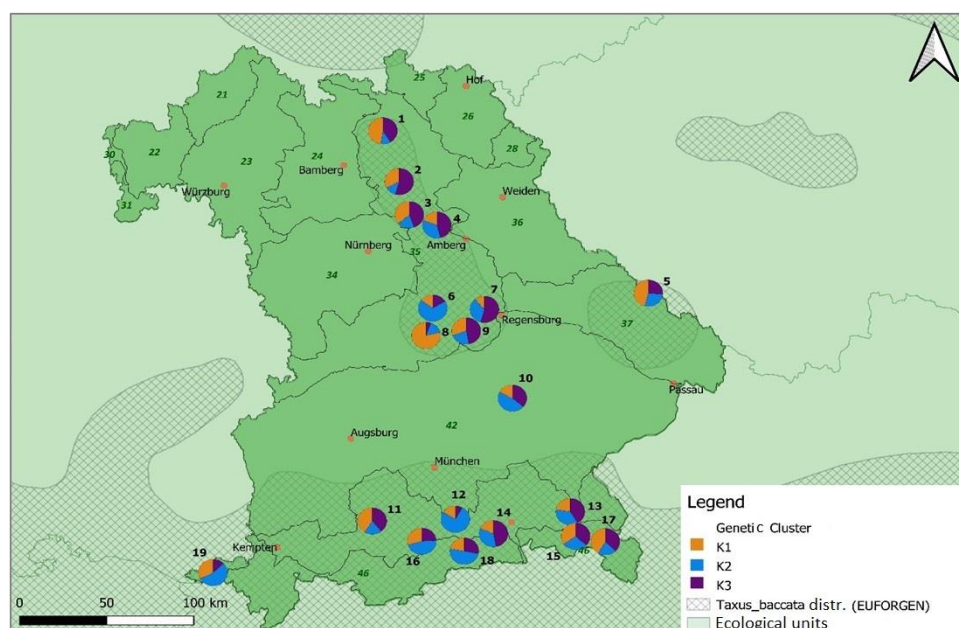
To determine possible clustering between the examined populations, the Bayesian model-based cluster algorithm was used. The maximum deltaK value (deltaK = 5.39) indicated the existence of 3 separate genetic clusters (Figures 3, 4 and Suppl. Figure 4).



**Figure 3.** Histogram of the genetic structure of English yew in Bavaria based on Bayesian clustering with STRUCTURE 2.3.3 software (Evanno et al., 2005). The four colors represent different STRUCTURE clusters. Populations are separated by vertical lines and identified on the X-axis by numbers (each individual is a separate color line). The column height of each color in the Y-axis corresponds to the probability of individual assignment to a different cluster separated by the STRUCTURE software. Structuring was performed based on 13 loci for  $K=3$ .

Figure 3 shows the result of cluster formation based on the 13 isoenzyme gene loci used and a K value of 3. Three colors represent the different STRUCTURE clusters. Figure 4 below

gives a comprehensive overview of the spatial-genetic structures in Bavaria.



**Figure 4.** Population genetic structure based on Bayesian clustering (STRUCTURE 2.3.3). The pie charts show the relative proportions of four STRUCTURE clusters.

## Discussion and Conclusion

Under climate change conditions the focus increase on rare native tree species such as white elm, field maple, service tree and English yew, which can be used as possible alternatives. However, the major challenge for successful species use is not sufficient the high-quality seed supply. Since these rare tree species are not subject to the German Forest Reproductive Material Act (FoVG, 2003) and mostly played a secondary role in silviculture, no suitable seed stands have been selected so far. Due to the two-stage procedure, important phenotypic characteristics such as quality, vitality, age, sex ratio and the number of trees as well as genetic parameters (structure, variety, and diversity) could be used for the selection and evaluation. Genetic diversity, differentiation and structure of the populations should build the basis for the conservation of FGR and the sustainable use of English yew.

### *Genetic Diversity, Differentiation and Structure in Taxus baccata Populations*

Isozyme analyses have been widely employed in studying the genetic structure and variation of English yew (e.g., Lewandowski et al., 1992; Hertel, 1996; Rajewski et al., 1999; Tröber & Ballian, 2011). Results of the genetic analyses are important to acquire baseline data for the implementation of gene conservation measures and GCU selection (Hattemer, 1995; Petit et al., 1998; Rajora & Mosseler, 2001; Caballero et al., 2010; etc.). In addition, to genetic information, an important

is phenotypical assessment, which can supplement existing knowledge on English yew (e.g., Tumpa et al., 2022).

In our study, genetic variation within and between the populations and their genetic structure was analyzed in 19 natural populations of English yew in Bavaria (Germany), using isozyme analyses at 13 gene loci. The study aimed at developing recommendations concerning the future use and genetic conservation strategies for the species, based on species distribution and genetic variation. Our research showed that the differences in the allele frequencies between the examined populations can be rated as very high. English yew populations in Bavaria are characterized by a moderately low level of genetic diversity (i.e., means of  $N_a = 2.28$ ,  $N_e = 1.61$ ,  $A_r = 2.24$  and  $H_e = 0.295$ ), and relatively high differentiation between English yew populations ( $F_{ST} = 0.09$ ). In comparison with other studies on English yew populations throughout Europe we found moderate values in genetic variability and relatively high genetic differentiation (Zarek, 2009; Tröber & Ballian, 2011; Klumpp & Dhar, 2011). Several studies on the genetic structure of English yew in Europe using different marker systems demonstrated a high level of overall genetic variation and significant differentiation between populations (Lewandowski et al., 1995; Cao et al., 2004; Hilfiker et al., 2004; Myking et al., 2009; Dubreuil et al., 2010; Tröber & Ballian, 2011; Chybicki et al., 2012). Myking et al. (2009) observed that the average observed ( $H_o$ ) and expected ( $H_e$ ) heterozygosities in the northern marginal populations were 0.143 and 0.150, respectively. In that investigation, the fixation index ( $F_{IS}$ )

across all populations was 0.039, but with consistently higher values (0.119 - 0.226) in the northernmost populations, suggesting inbreeding (Myking et al., 2009). In our study, the average observed and expected heterozygosity was slightly higher  $H_o = 0.291$  and  $H_e = 0.295$ . The inbreeding coefficient ( $F_{IS}$ ) was lower than 0.012. A similar result ( $N_e = 1.41$ ,  $H_o = 0.28$ ,  $H_e = 0.29$ ) was found at the national level in the project with the aim of identifying genetic resources of field maple (*Acer campestre* L.) and yew (*Taxus baccata* L.) in Germany (Riederer & Fritsch, 2013). Tröber and Balian (2011) observed higher values for observed and expected heterozygosity of two Bosnian populations in Ozren ( $H_a = 0.490$  and  $H_e = 0.334$ ) and Borja ( $H_a = 0.367$  and  $H_e = 0.361$ ) in comparison with the results of our study.

Furthermore, the extensive sampling design in our study allowed us to infer the spatial genetic structure of the sampled populations. By applying Bayesian clustering we detected the existence of three genetic clusters ( $K = 3$ ,  $\Delta K = 5.390$ ) within 19 studied English yew populations in Bavaria (Figures 3 and 4). Part of the spatial genetic pattern can be attributed to the species' ecology (association with covered forest ecosystems) and scattered distribution. However, population 8 have formed a clearly separate genetic cluster (Figures 3 and 4), which can be explained by the artificial introduction of several plants (the founder effect) and/or by isolation and genetic drift. The groups shown in the histogram (see Figure 3) cannot be clearly separated spatially. The pie charts reflect the relative affiliation to the three STRUCTURE clusters and are spatially mixed. It is therefore recommended to designate only one provenance region for *Taxus baccata* L. in Bavaria. Furthermore, knowledge regarding English yew population differentiation and diversity allows us the recommendation of seed stand selection and planning of GCU and conservation measures in Bavaria.

### Selection of English yew GCUs in Bavaria

Genetic conservation activities of rare tree species such as English yew need to consist of several main steps: (i) species distribution inventory; (ii) GCU and plus trees (*in situ* protection) selection for conservation; and (iii) *ex situ* genetic resources establishment e.g., seed orchards, collections in a gene bank, etc. (e.g., Hemery et al., 2010; Koskela et al., 2013; Kavaliauskas et al., 2021). Protection of small populations and single trees is vital to ensure gene flow among populations. Known populations of English yew must be preserved through active management, and trees should be introduced into new sites to increase gene flow and reduce spatial isolation.

The information on genetic variation and structure of English yew populations in Bavaria provides a background for the implementation of FGR conservation programmes and seed stand selection. The main criteria for GCU selection should be high genetic diversity which ensures the possibility for populations to evolve and reproduce under changing

environmental conditions. Many authors identify allelic richness ( $A_r$ ) as a key parameter for conservation purposes in genetic conservation programs, especially for rare tree species of subdivided various in size populations (Marshall & Brown, 1975; Petit et al., 1998; Rajora et al., 2000; Rajora & Mosseler, 2001; Caballero et al., 2010; etc.). Therefore, in our study, we used allelic diversity ( $A_r$ ) between and within populations for populations prioritization for conservation and English yew GCU selection (Petit et al., 1998; Caballero et al., 2010; Kavaliauskas et al., 2021).

The results of our study showed that allelic richness varies slightly across the investigated populations and ranged between 2.11 (8-Zandt) and 2.44 (10- Landshut). Six sampled populations exhibit higher than average allelic richness ( $A_r \geq 2.24$ ) based on 13 isoenzyme loci (Table 2). Thus, populations with moderate allelic richness ( $A_r > 2.20$ ) can be considered as GCUs in Bavaria. However, we proposed to approve 11 populations as GCUs. The selected 11 populations are distributed across Bavaria representing several different ecological zones. Additional criteria for GCU selection were a sufficient number of trees and distribution over the stand, vitality, reproductive age, information about the origin, etc.

Following our experience, we think that further selection of GCUs for rare tree species should be constructed on collective parameters of environmental and genetic diversity data, considering population distribution in certain regions. Marginal populations at the species distribution edge tend to exhibit higher genetic differentiation in comparison to populations from the main distribution, therefore some differentiation indexes such as Nei (1972)'s can be an additional parameter for GCU selection (Petit et al., 1998). However, genetic differentiation results vary depending on the type and the number of genetic markers used. Since Bavaria is at the distribution edge of *Taxus baccata*, the representative selection [three populations (1, 2 and 4) from the north of Bavaria, three (5, 9 and 10) from mid-Bavaria, and five (11, 12, 13, 16 and 17) from the southeast of Bavaria, representing two main STRUCTURE clusters] of putative GCUs in Bavaria was an important step ensuring species conservation measures under changing environmental conditions.

Overall, our research revealed that English yew populations in Bavaria are characterized by moderate genetic diversity (i.e., expected heterozygosity and number of effective alleles). Similar diversity parameters are reported in other studies on *Taxus baccata* (e.g., Zarek, 2009, Tröber & Ballian, 2011, Klumpp & Dhar, 2011, Myking et al., 2009), which can be explained by species ecology and other peculiarities; however, it is important to implement conservation measures and to maintain genetic diversity for the long-term adaptation of populations to changing environmental and climatic conditions. Furthermore, at the European level, 57 GCUs (Gene Conservation Units) of *Taxus baccata* are included in the



European genetic conservation network within the EUFORGEN program. And only five populations, two in Thuringia, one in Saxony and two in Bavaria, in Germany. Thus, considering the results from our analysis, at least a few more populations representing different environmental conditions should be included in the GCU network covering the whole English yew distribution range in Bavaria.

### English Yew Seed Stand Selection

Selection of seed stands, and other in-situ conservation measures is an important step under rapid climate change in preserving and increasing genetic diversity and supporting species adaptability. Because the English yew is not listed in FoVG (2003) or in the EU directive 1999/105/CE (EU, 1999), there are no official requirements and regulations for English yew seed stand selection, FRM collection and trade. Therefore, genetic structure and diversity data deliver important information on English yew genetic status in Bavaria and allow us to perform the selection of seed stands according to collective parameters in a representative manner. In our study, the mean number of effective alleles ( $N_e$ ) was used as a measure for seed stand selection in Bavaria.  $N_e$  value shows the level of genetic diversity within a population and includes the distribution and frequency of the alleles (Kimura & Crow, 1964; Maruyama, 1970). Since the differences in genetic diversity parameters ( $N_a$ ,  $N_e$ ,  $A_r$ ,  $H_o$  and  $H_e$ ) was low among the populations (Table 2), only two populations were not selected as seed stand (pop. 1-Schammendorf, pop. 8 Zandt). Population which was specified by the forest district managers as possibly planted exhibited lower values of genetic diversity (e.g.,  $N_e$ ,  $A_r$ , and  $V_{gam}$ ) than the overall mean. However, in specific circumstances all studied populations can be considered for seed collection with the recommendation to increase the number of seed trees to collect from. Especially if allelic richness is higher, the lower number of effective alleles can be increased by more intensive and representative sampling/seed tree selection.

Following the results of our study for the rare tree species field maple (*Acer campestre* L.), European white elm (*Ulmus laevis* Pall.), service tree (*Sorbus domestica* L.) and English yew (*Taxus baccata* L.) and based on study by Kavaliauskas et al. (2021) in Bavaria we propose several important preconditions for seed stand selection and seed collection:

- Minimum number of trees: at least 30 seed trees have to be selected for seed collection.
- Seed tree distribution: selected seed trees should be distributed over the whole of the seed stand, to ensure representative seed collection and the highest genetic variation.
- Genetic diversity: selected seed stands have to contain high genetic diversity; thus, genetic markers have to be

applied to provide additional information in the process of stand selection.

Seed stand selection involves the consideration of various factors and according to Neel and Cummings (2003), if selection of seed stands and GCUs are made without genetic knowledge, then a larger number and larger populations are required to ensure high genetic diversity and representation of alleles. In our study, a total of 17 stands which fulfilled the genetic diversity and stand quality requirements were proposed as potential seed stands. Furthermore, results on genetic diversity provide us with additional information on the genetic status and variation among stands and form a basis for comparison of potentially new seed stands in further stand selection (Namkoong, 1984). In addition, to improve English yew conservation actions, selected GCUs that are among selected seed stands should be included in the EUFORGEN / EUFGIS (<http://portal.eufgis.org/>) GCU network to cover and represent different environments at the country level. Finally selected seed stands provide a basis for obtaining seed of higher genetic quality until material from more intensively selected trees in seed orchards will be available.

Overall, successful selection of high-quality forest genetic resources (FGR) is an important part of the Concept for the conservation and the sustainable use of forest genetic resources in Bavaria (Konnert et al., 2015). Therefore, our study of English yew populations in Bavaria is an important contribution to this concept and a further step towards securing FGR of scattered tree species in Germany. Furthermore, increasing interest in rare tree species and mixed forest formation by state and private forest owners is important for conservations of endangered tree species such as English yew. After completion of the project, the selected seed stands, and gene conservation units will be included in the Bavarian Forest reproductive information system (EZR) and thus made available for access by all seed harvesting companies and forest tree nurseries. This ensures long-term use of these valuable survey. The forest reproductive material produced from the seed stands recommended here can be used outside of forestry, as autochthonous ("gebietseigene") woody plants. The use of native provenances is also demanded by German law: according to § 41 of the Federal Nature (BMU, 2009). In addition, it is planned to establish seed orchards for the four project tree species in the coming years. The first 19 plus trees were already selected and 50-60 trees more to come to establish a clonal seed orchard.

### Conflict of Interest

The authors declare that they have no conflict of interest.

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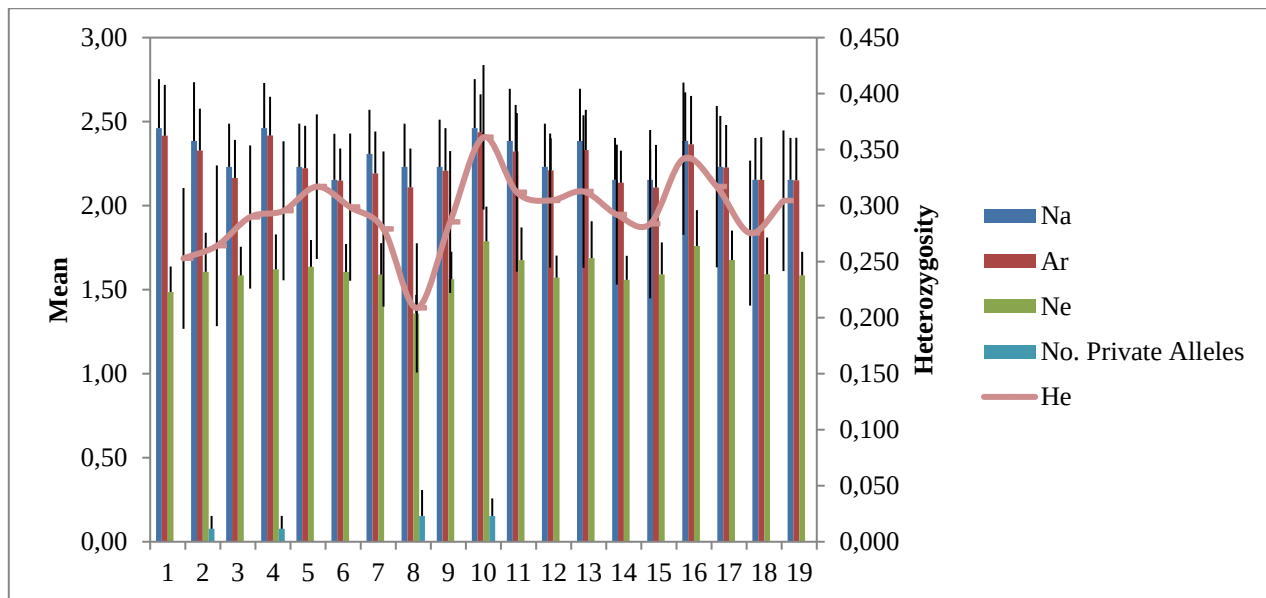
## Supplementary Information



**Supplementary Figure 1.** Natural and introduced distribution area of *Taxus baccata* in Europa after Caudullo et al. (2017); Green: Native range and isolated population, Brown: Introduced and naturalized (synanthropic) area and isolated population.

**Supplementary Table 1.** Allele frequencies at 13 isoenzyme loci in the 19 English yew populations

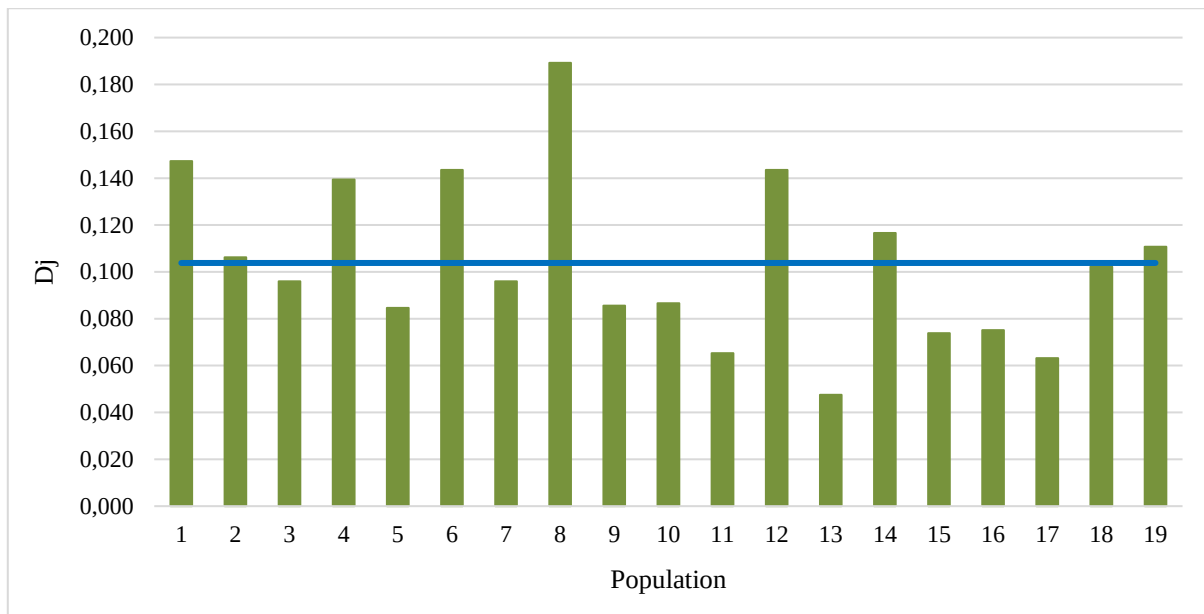
| Genort | Population |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |
|--------|------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
|        | 1          | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    | 10   | 11   | 12   | 13   | 14   | 15   | 16   | 17   | 18   | 19   |
| pgib1  | 0,28       | 0,29 | 0,44 | 0,29 | 0,49 | 0,19 | 0,08 | 0,89 | 0,25 | 0,29 | 0,31 | 0,61 | 0,24 | 0,02 | 0,34 | 0,36 | 0,31 | 0,23 | 0,56 |
| pgib2  | 0,06       | 0,21 | 0,10 | 0,18 | 0,08 | 0,03 | 0,21 | 0,02 | 0,23 | 0,21 | 0,08 | 0,15 | 0,26 | 0,21 | 0,08 | 0,24 | 0,03 | 0,24 | 0,11 |
| pgib3  | 0,13       | 0,26 | 0,11 | 0,35 | 0,19 | 0,51 | 0,33 | 0,09 | 0,07 | 0,19 | 0,28 | 0,21 | 0,20 | 0,24 | 0,31 | 0,19 | 0,21 | 0,21 | 0,08 |
| pgib4  | 0,53       | 0,24 | 0,35 | 0,18 | 0,24 | 0,27 | 0,38 | 0,00 | 0,45 | 0,31 | 0,32 | 0,03 | 0,30 | 0,53 | 0,27 | 0,20 | 0,45 | 0,31 | 0,25 |
| idha1  | 0,11       | 0,27 | 0,31 | 0,41 | 0,11 | 0,24 | 0,32 | 0,08 | 0,23 | 0,27 | 0,18 | 0,26 | 0,22 | 0,07 | 0,21 | 0,28 | 0,21 | 0,14 | 0,31 |
| idha2  | 0,82       | 0,56 | 0,54 | 0,51 | 0,75 | 0,53 | 0,59 | 0,75 | 0,70 | 0,63 | 0,66 | 0,61 | 0,66 | 0,90 | 0,66 | 0,55 | 0,64 | 0,77 | 0,65 |
| idha3  | 0,07       | 0,16 | 0,14 | 0,07 | 0,14 | 0,03 | 0,00 | 0,16 | 0,04 | 0,09 | 0,15 | 0,11 | 0,08 | 0,00 | 0,13 | 0,10 | 0,16 | 0,09 | 0,04 |
| idha4  | 0,00       | 0,01 | 0,01 | 0,01 | 0,00 | 0,20 | 0,09 | 0,01 | 0,03 | 0,01 | 0,02 | 0,01 | 0,04 | 0,03 | 0,00 | 0,07 | 0,00 | 0,00 | 0,00 |
| idhb1  | 0,00       | 0,00 | 0,00 | 0,04 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| idhb2  | 0,05       | 0,00 | 0,09 | 0,06 | 0,04 | 0,27 | 0,00 | 0,00 | 0,01 | 0,10 | 0,01 | 0,23 | 0,05 | 0,27 | 0,12 | 0,17 | 0,00 | 0,04 | 0,10 |
| idhb3  | 0,95       | 1,00 | 0,91 | 0,90 | 0,96 | 0,73 | 1,00 | 0,85 | 0,99 | 0,90 | 0,99 | 0,78 | 0,95 | 0,73 | 0,88 | 0,83 | 1,00 | 0,96 | 0,90 |
| idhb4  | 0,00       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,05 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| idhb5  | 0,00       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,10 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| pgma1  | 0,14       | 0,03 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,02 | 0,00 | 0,01 | 0,00 | 0,01 | 0,02 | 0,04 | 0,00 | 0,00 |
| pgma2  | 0,19       | 0,12 | 0,12 | 0,09 | 0,17 | 0,00 | 0,01 | 0,01 | 0,14 | 0,29 | 0,20 | 0,04 | 0,21 | 0,23 | 0,20 | 0,36 | 0,19 | 0,20 | 0,16 |
| pgma3  | 0,06       | 0,02 | 0,00 | 0,12 | 0,15 | 0,11 | 0,01 | 0,39 | 0,15 | 0,03 | 0,11 | 0,01 | 0,06 | 0,14 | 0,01 | 0,07 | 0,06 | 0,04 | 0,18 |
| pgma4  | 0,60       | 0,83 | 0,88 | 0,79 | 0,68 | 0,89 | 0,98 | 0,60 | 0,71 | 0,68 | 0,68 | 0,95 | 0,72 | 0,63 | 0,78 | 0,55 | 0,70 | 0,76 | 0,66 |
| p6a1   | 0,34       | 0,32 | 0,46 | 0,21 | 0,45 | 0,80 | 0,38 | 0,75 | 0,34 | 0,45 | 0,54 | 0,46 | 0,48 | 0,34 | 0,65 | 0,69 | 0,42 | 0,83 | 0,78 |
| p6a2   | 0,66       | 0,68 | 0,54 | 0,79 | 0,55 | 0,20 | 0,62 | 0,25 | 0,66 | 0,55 | 0,46 | 0,54 | 0,52 | 0,66 | 0,35 | 0,31 | 0,58 | 0,17 | 0,22 |
| adha1  | 0,16       | 0,11 | 0,23 | 0,09 | 0,15 | 0,04 | 0,02 | 0,21 | 0,07 | 0,00 | 0,24 | 0,00 | 0,02 | 0,02 | 0,05 | 0,03 | 0,18 | 0,06 | 0,06 |
| adha2  | 0,07       | 0,03 | 0,01 | 0,33 | 0,03 | 0,35 | 0,25 | 0,15 | 0,09 | 0,44 | 0,07 | 0,51 | 0,31 | 0,10 | 0,08 | 0,25 | 0,13 | 0,39 | 0,35 |
| adha3  | 0,77       | 0,84 | 0,76 | 0,58 | 0,82 | 0,61 | 0,73 | 0,64 | 0,84 | 0,56 | 0,69 | 0,49 | 0,67 | 0,88 | 0,87 | 0,72 | 0,68 | 0,56 | 0,59 |
| adha4  | 0,00       | 0,01 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| mnra1  | 0,69       | 0,68 | 0,49 | 0,17 | 0,50 | 0,43 | 0,49 | 0,27 | 0,31 | 0,53 | 0,59 | 0,43 | 0,37 | 0,39 | 0,51 | 0,38 | 0,42 | 0,16 | 0,23 |
| mnra2  | 0,11       | 0,03 | 0,00 | 0,01 | 0,02 | 0,00 | 0,01 | 0,00 | 0,00 | 0,00 | 0,01 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,11 | 0,00 | 0,00 |
| mnra3  | 0,20       | 0,29 | 0,51 | 0,82 | 0,48 | 0,57 | 0,50 | 0,73 | 0,69 | 0,47 | 0,40 | 0,58 | 0,63 | 0,61 | 0,49 | 0,63 | 0,47 | 0,84 | 0,77 |
| aata2  | 1,00       | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 |
| aata1  | 0,08       | 0,05 | 0,11 | 0,07 | 0,36 | 0,38 | 0,13 | 0,01 | 0,15 | 0,19 | 0,17 | 0,83 | 0,13 | 0,25 | 0,13 | 0,25 | 0,27 | 0,19 | 0,41 |
| aata2  | 0,91       | 0,95 | 0,89 | 0,93 | 0,64 | 0,62 | 0,86 | 0,99 | 0,85 | 0,81 | 0,83 | 0,18 | 0,87 | 0,75 | 0,87 | 0,75 | 0,73 | 0,81 | 0,59 |
| aata3  | 0,01       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,01 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| mdhc2  | 1,00       | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 | 1,00 |
| sdhb1  | 0,00       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,01 | 0,00 | 0,00 | 0,01 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| sdhb2  | 1,00       | 0,97 | 0,93 | 0,91 | 0,88 | 0,96 | 0,87 | 1,00 | 0,89 | 0,65 | 0,95 | 0,93 | 0,92 | 0,97 | 1,00 | 0,95 | 0,97 | 0,94 | 0,97 |
| sdhb3  | 0,00       | 0,03 | 0,07 | 0,09 | 0,12 | 0,04 | 0,13 | 0,00 | 0,11 | 0,33 | 0,05 | 0,08 | 0,07 | 0,03 | 0,00 | 0,05 | 0,03 | 0,06 | 0,03 |
| lapa1  | 0,03       | 0,00 | 0,01 | 0,07 | 0,00 | 0,00 | 0,01 | 0,01 | 0,00 | 0,00 | 0,00 | 0,04 | 0,00 | 0,00 | 0,00 | 0,01 | 0,00 | 0,00 | 0,00 |
| lapa2  | 0,97       | 1,00 | 0,99 | 0,93 | 1,00 | 1,00 | 0,99 | 0,99 | 1,00 | 0,97 | 1,00 | 0,96 | 1,00 | 1,00 | 1,00 | 0,99 | 1,00 | 1,00 | 1,00 |
| lapa4  | 0,00       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,03 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| lapb1  | 0,01       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,03 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| lapb2  | 0,92       | 0,59 | 0,30 | 0,28 | 0,52 | 0,90 | 0,61 | 0,99 | 0,56 | 0,64 | 0,54 | 0,69 | 0,58 | 0,54 | 0,53 | 0,65 | 0,64 | 0,54 | 0,70 |
| lapb3  | 0,00       | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,01 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 | 0,00 |
| lapb4  | 0,07       | 0,41 | 0,70 | 0,72 | 0,48 | 0,10 | 0,39 | 0,01 | 0,44 | 0,32 | 0,46 | 0,31 | 0,42 | 0,46 | 0,47 | 0,35 | 0,36 | 0,46 | 0,30 |



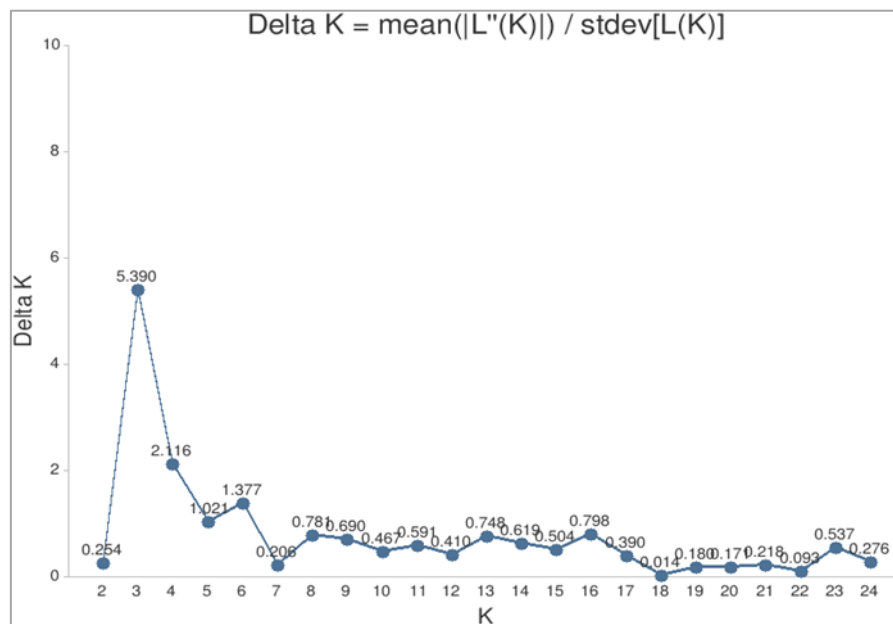
**Supplementary Figure 2.** The within-population genetic diversity parameters were estimated based on 13 isoenzyme loci [GeneAlex6.5 Software (Peakall & Smouse, 2012)].

**Supplementary Table 2.** Pairwise population matrix of Nei (1972) genetic distance (Software GeneAlex6.5)

| Pop_ID | 1    | 10   | 11   | 12   | 13   | 14   | 15   | 16   | 17   | 18   | 19   | 2    | 3    | 4    | 5    | 6    | 7    | 8    | 9    |
|--------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| 1      | 0,00 | 0,26 | 0,19 | 0,35 | 0,22 | 0,26 | 0,22 | 0,27 | 0,18 | 0,27 | 0,27 | 0,18 | 0,23 | 0,29 | 0,24 | 0,32 | 0,25 | 0,27 | 0,21 |
| 10     |      | 0,00 | 0,19 | 0,23 | 0,13 | 0,25 | 0,19 | 0,18 | 0,20 | 0,20 | 0,22 | 0,22 | 0,20 | 0,24 | 0,21 | 0,28 | 0,18 | 0,35 | 0,20 |
| 11     |      |      | 0,00 | 0,27 | 0,12 | 0,21 | 0,13 | 0,17 | 0,14 | 0,18 | 0,21 | 0,14 | 0,16 | 0,23 | 0,14 | 0,27 | 0,17 | 0,27 | 0,14 |
| 12     |      |      |      | 0,00 | 0,23 | 0,29 | 0,24 | 0,24 | 0,28 | 0,27 | 0,23 | 0,27 | 0,24 | 0,28 | 0,25 | 0,24 | 0,23 | 0,34 | 0,26 |
| 13     |      |      |      |      | 0,00 | 0,18 | 0,14 | 0,14 | 0,16 | 0,13 | 0,18 | 0,16 | 0,16 | 0,18 | 0,18 | 0,25 | 0,13 | 0,29 | 0,12 |
| 14     |      |      |      |      |      | 0,00 | 0,20 | 0,18 | 0,21 | 0,24 | 0,24 | 0,23 | 0,25 | 0,29 | 0,20 | 0,27 | 0,24 | 0,34 | 0,15 |
| 15     |      |      |      |      |      |      | 0,00 | 0,17 | 0,18 | 0,19 | 0,21 | 0,16 | 0,14 | 0,25 | 0,16 | 0,25 | 0,19 | 0,28 | 0,16 |
| 16     |      |      |      |      |      |      |      | 0,00 | 0,19 | 0,18 | 0,16 | 0,24 | 0,22 | 0,26 | 0,20 | 0,23 | 0,22 | 0,27 | 0,20 |
| 17     |      |      |      |      |      |      |      |      | 0,00 | 0,20 | 0,18 | 0,18 | 0,20 | 0,26 | 0,17 | 0,26 | 0,20 | 0,31 | 0,17 |
| 18     |      |      |      |      |      |      |      |      |      | 0,00 | 0,14 | 0,23 | 0,23 | 0,19 | 0,22 | 0,24 | 0,22 | 0,30 | 0,18 |
| 19     |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,26 | 0,24 | 0,23 | 0,20 | 0,21 | 0,26 | 0,26 | 0,19 |
| 2      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,16 | 0,21 | 0,18 | 0,30 | 0,16 | 0,31 | 0,13 |
| 3      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,20 | 0,18 | 0,30 | 0,18 | 0,33 | 0,18 |
| 4      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,27 | 0,31 | 0,22 | 0,34 | 0,21 |
| 5      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,29 | 0,21 | 0,30 | 0,15 |
| 6      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,25 | 0,30 | 0,29 |
| 7      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,34 | 0,16 |
| 8      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 | 0,28 |
| 9      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      |      | 0,00 |



**Supplementary Figure 3.** Differentiation ( $D_j$ ) of the 19 populations studied. The blue line indicates the mean differentiation of all populations at the level of 10%.



**Supplementary Figure 4.** The results of Bayesian clustering [software STRUCTURE 2.3.3 (Pritchard et al., 2000)] on the most likely number of genetic clusters within the studied English yew populations, indicated by the highest delta K value at K = 3 [software CLUMPAK (Kopelman et al., 2015)].