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High Genetic Differentiation in Marginal Populations of European White Elm (*Ulmus laevis*)

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Studies on the amount of genetic variation in marginal populations and differentiation between them are essential for assessment of best gene conservation strategies and sampling schemes. Thirteen marginal populations of *Ulmus laevis* in southern Finland and one in Estonia were investigated for genetic variation in 20 allozyme loci. Population differentiation among Finnish stands was high, $F_{st}=0.290$, and mean genetic diversity low, $H_e=0.088$. The differentiation follows the isolation-by-distance structure within the core of the distribution area (lake Vanajavesi). Fairly high frequency of recurrent genotypes was observed, but this did not have an influence on the genetic parameters. The observed genetic structure is consistent with the central-marginal hypothesis. In the light of the results, the Finnish gene conservation strategy for *U. laevis* seems to be on a sound basis.

Keywords genetic differentiation, marginal populations, genetic conservation, *Ulmus*
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1 Introduction

European forests generally include few dominant tree species with wide habitat preferences but also other tree species with restricted and scattered distribution. The distribution of the less common species is restricted due to specific niches, and unfortunately in many cases, these habitats have become rarer due to human impact. Among the most threatened habitats in Europe are riparian forests that have decreased drastically due to e.g. control of river dynamics, wood logging and grazing. Recently various measures including targeted research programmes and conservation and restoration plans have been taken to avoid complete disappearance of riparian forests (Lefevre et al. 2002, Hughes and Rood 2003). In addition to attempts to maintain habitat biodiversity, genetic

biodiversity of species and populations growing in threatened habitats should be taken into account. Enough genetic variation within populations is needed to meet challenges due to rapid climate change with possibly increasing abiotic and biotic stresses. Furthermore, new applications of forest trees e.g., in medicine and food industry (e.g. Jung et al. 2008) also put pressure on research and conservation plans of gene resources of forest trees.

Depending on the taxon concerned, different strategies have been adopted for the practical gene conservation, the main choice being between ex situ and in situ based approaches. Basic problem in the both types is the selection of populations to be included in the programme, and if ex situ is applied, how many individuals should be sampled from each of the chosen populations. General sampling strategies have been discussed e.g. in Eriksson et al. (1993). In many species, however, the present knowledge on ecology and genetics of populations is so limited that most efficient and cost-effective conservation methods can be designed only after basic genetic studies.

European white elm (*Ulmus laevis* Pall.) is a deciduous temperate forest tree species distributed across central and east Europe. The distribution extends from Ural mountains in the east to France in the west and from southern Finland in the north to Bosnia in the south, and it is considered rare in most of these areas or endangered (Collin 2002). White elm is a riparian species, typically found on river banks, lake shores and other moist sites, but it can also tolerate dry soils of wooded steppe habitat in the central parts of the distribution. Seeds are dispersed by wind, but in the riparian habitats also by floating, which enables long-distance colonisations.

In Finland, *U. laevis* is growing at northwestern margin of the species' distribution, fairly isolated from the main distribution (Collin 2003). The closest populations to Finnish ones are located in Estonia and north-eastern Russia, several hundred kilometres apart from the Finnish stands. White elm is quite rare with very restricted distribution in Finland and it is regarded as an endangered species. About 7000 trees, including saplings, have been estimated to grow along a lake and river system in southern Finland, within an area of 20 km × 100 km (Uotila 2000). In addition, two populations and some individual trees are found outside this main area. The species is protected by the Nature Conservation Decree (160/1997) and also some of the populations grow in nature conservation areas. In addition to species and habitat conservation, *U. laevis* is one of the target species in the National Gene Conservation Program, where dynamic ex situ conservation in grafted clonal collections is the main tool for conserving genetic variability in *Ulmus* species (Suomen maa- ja metsätalouden… 2002).

Along with many other wetland species, European white elm (*U. laevis*) has decreased in numbers while suitable habitats have grown scarce due to the increasing water-basin regulation and demand of agricultural land. An additional threat for elm populations is an alien, hypervirulent pathogen, *Ophistoma novo ulmi*, the agent of Dutch Elm Disease (DED), which has severely attacked populations of *U. laevis* especially in the central and eastern Europe (Collin 2003). For these reasons, elms in general have received special attention in forest inventories of most of the European countries and a number of conservation measures have been initiated (Eriksson, 2001, Collin et al. 2004). However, relative little is yet known on the patterns of genetic variation in elm species, especially in the northernmost marginal populations that have not so far suffered from DED.

In this paper we describe the patterns of genetic variation in the northern marginal populations of *U. laevis* in southern Finland. We study how much random genetic drift has decreased within-population variation, search for signs of increased inbreeding and increased between-population variation, and discuss the implications of the results to the Finnish gene conservation program.

2 Material and Methods

2.1 Study Populations and Sampling

Dormant winter buds were sampled from 13 natural populations of European white elm (*U. laevis*) in southern Finland (Fig. 1) and one population in Estonia. The buds were kept at –20 °C until analysis. The exact locations of sampled populations are presented in Table 1. The sampling covers the natural distribution of the species in Finland. All

Table 1. Latitude, longitude, sample size (n), population size (N), percentage of polymorphic loci at 95% (P95), number of alleles (A), number of alleles in polymorphic loci (AP), allelic richness at sample size 20 (AR), expected heterozygosity (H_e), observed heterozygosity (H_o) and fixation index (F_{is}). For H_e, H_o and F_{is}, separate estimates are shown for all samples (1st) and for unique genotypes only (2nd), separated by a slash. Statistically significant F_{is} values are indicated by an asterisk. Mean is calculated over the Finnish populations.

	Population	Commune	Latitude	Longitude	n	N	P95	A	Ap	AR	H_e	H_o	F_{is}
1	Retulansaari	Hattula	61°11´	24°20´	25	>100	0.20	1.25	2.25	1.25	0.089/0.093	0.092/0.093	–0.035/-0.009
2	Ikkala	Valkeakoski	61°11´	24°12´	32	32	0.20	1.30	2.25	1.30	0.088/0.095	0.089/0.086	–0.013/0.101
3	Annila	Valkeakoski	61°12´	24°02´	44	>50	0.30	1.45	2.33	1.39	0.123/0.126	0.126/0.125	–0.025/0.006
4	Ruskeankärki	Hattula	61°07´	24°15´	14	14	0.25	1.25	2.00	-	0.088/0.092	0.093/0.100	–0.069/-0.098
5	Sääksmäki	Valkeakoski	61°11´	24°02´	24	24	0.20	1.35	2.00	1.33	0.080/0.099	0.085/0.100	–0.067/-0.008
6	Kalalahti	Toijala	61°11´	23°58´	39	50	0.20	1.25	2.00	1.23	0.054/0.064	0.058/0.061	–0.063/0.043
7	Saarela	Hattula	61°03´	24°25´	50	51	0.30	1.40	2.17	1.35	0.110/0.113	0.106/0.101	0.044/0.103
8	Lotilanjärvi	Valkeakoski	61°15´	24°00´	39	50	0.15	1.20	2.00	1.20	0.050/0.060	0.056/0.057	–0.121*/0.059
9	Kirkkojärvi	Lempäälä	61°20´	23°44´	44	45	0.35	1.45	2.29	1.43	0.144/0.147	0.137/0.135	0.052/0.083
10	Pirkkala	Nokia	61°28´	23°36´	45	47	0.25	1.25	2.00	1.25	0.085/0.080	0.077/0.080	0.095/0.004
11	Urmia	Nokia	61°28´	23°32´	54	53	0.25	1.30	2.20	1.30	0.086/0.096	0.097/0.098	–0.132*/–0.021
12	Jalassaari	Lohja	60°13´	23°53´	46	50	0.25	1.40	2.20	1.35	0.079/0.097	0.077/0.087	0.016/0.106
13	Tesjoki	Ruotsinpyhtää	60°28´	26°02´	21	28	0.20	1.20	2.00	1.20	0.069/0.075	0.085/0.072	–0.243*/0.046
	Mean						0.24	1.31	2.13	1.30	0.088/0.095	0.091/0.092	–0.043/0.035
Helmejoki		Estonia	58°01´	25°52´	46		0.30	1.50	2.33	1.44	0.139	0.136	0.017

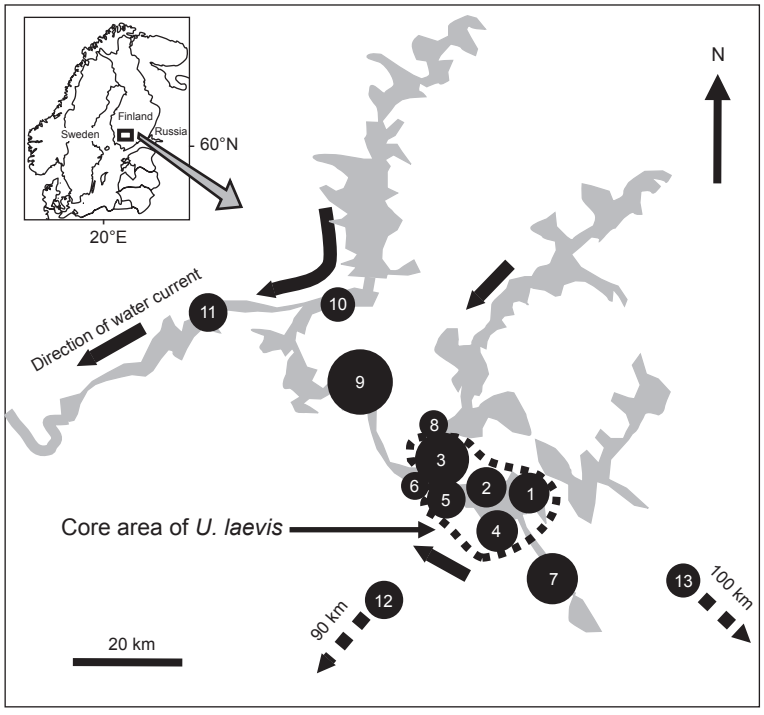

Fig. 1. Location of the sampled Finnish *Ulmus laevis* populations. Numbers within the circles refer to the population numbers in Table 1. Diameter of the circle is proportional to the expected heterozygosity of the population.

the populations within Kokemäenjoki rivershed (populations 1–11) were regarded as the main distribution area. Within this area, populations 1–5 on the shores of lake Vanajavesi were handled as a separate group representing the core of natural distribution. Populations 6 and 8 are located on the shores of separate lakes and thus not included in the core. These two subsets are later referred to as main and core, respectively. In small populations ($N < 50$) all the mature trees, and in large populations about 50 randomly selected trees, were sampled. The approximate population sizes, detailed location of populations and number of trees analysed are given in Table 1.

2.2 Electrophoresis

Bud scales were removed and tissue from three or four buds per tree was homogenized in 3–4 drops of 0.1 M Tris-HCl extraction buffer pH 7.5 (Bousquet et al. 1987), modified by omitting polyethylene glycol. Allozyme variation in the populations was analysed at 20 loci: LAP1 and LAP2 (leucine aminopeptidase, E.C. 3.4.11.1), GOT1 and GOT2 (glutamate-oxaloacetate transaminase E.C. 2.6.1.1), ADH (alcohol dehydrogenase E.C. 1.1.1.1), PGI1 and PGI2 (phosphoglucoisomerase E.C. 5.3.1.9), SDH (shikimate dehydrogenase E.C. 1.1.1.25), IDH (isocitrate dehydrogenase E.C. 1.1.1.41), FEST (fluorescent esterase E.C. 3.1.1.1), GDH (glutamate dehydrogenase E.C. 1.4.1.3), 6-PGD1 and 6-PGD2 (6-phosphogluconate dehydrogenase E.C.1.1.1.44), MDH1 and MDH2 (malate dehydrogenase E.C. 1.1.1.37), ACO (aconitase E.C. 4.2.13), DIA (diaphorase E.C.1.6.4.3), PGM (phosphoglucomutase E.C. 5.4.2.2), PER (peroxidase E.C. 1.11.1.7) and SOD (superoxide dismutase E.C.1.15.1.1).

Standard starch gel electrophoresis (12% Sigma Hydrolyzed Starch) and three buffer systems were used: Ashton pH 8.1 (Ashton and Braden 1961)

and Tris-citrate pH 7.1 and pH 7.8 (Shaw and Prasad 1970). Enzyme activity staining protocols were according to Cheliak and Pitel (1984) with slight modifications. Genetic interpretation of the isozymes and alleles was based on their sub-unit structure, and on assumed Mendelian inheritance and codominance.

2.3 Statistical Analyses

Basic population genetic parameters, i.e. the proportion of polymorphic loci at the 95% level (P95), number of alleles per locus (A), number of alleles per polymorphic loci (AP), allelic richness (AR; Petit et al 1998), expected (H_e) and observed (H_o) heterozygosity, genetic distance (Nei 1978) and F-statistics (F_{st}, F_{is}) according to Weir and Cockerham (1984), were calculated using GDA software (Lewis and Zaykin 2001) and FSTAT ver 2.9.3.2 (Goudet 1995) for all populations using 20 loci. Statistical significance of the differences between the regions in the genetic parameters was tested by ANOVA. Confidence intervals for F_{st} estimates were obtained by bootstrapping over the loci (Weir 1996). Correlations between pairwise genetic distance and respective map distance was assessed by simple Mantel tests in FSTAT ver 2.9.3.2 (Goudet 1995), separately for all populations, main area and core area.

Due to possibility of clonal propagation in populations, identical genotypes within each population were identified and number of individuals with each recurrent genotype was calculated. The probability of a second encounter by sexual reproduction was estimated according to Parks and Werth (1993) for the genotypes with two or more individuals. Without Bonferroni correction, the probability <0.05 was regarded to indicate a significant deviation from random mating. Using Bonferroni correction, the critical value was divided by the total number of recurring genotypes. The expected number of observations for each recurrent genotype was estimated using the expectation of binomial distribution. Basic genetic diversity parameters and population differentiation were estimated for a subset of data with unique genotypes only. The subset of unique genotypes was created by including only one sample representing each multilocus genotype.

3 Results

Out of the 20 scored loci 8 were polymorphic in at least one population, the proportion of polymorphic loci ranging from 15% to 35% (Table 1). No unique alleles were detected. Expected heterozygosity (H_e) was quite variable ranging from 0.050 to 0.144 with an average of 0.088 for the Finnish populations (Table 1). None of the genetic diversity statistics were significantly different between groups of core area and other populations. The genetic diversity estimates for the Estonian population (Helmejoki) are on the upper limit of the Finnish populations. The fixation index F_{is} was mostly negative and in three populations (8, 11 and 13) F_{is} was statistically significant when estimated for all trees (Table 1). For unique genotypes, F_{is} estimates were not statistically significant from zero.

Population differentiation among Finnish stands was significantly different from zero ($F_{st}=0.290$ for the whole data and $F_{st}=0.227$ for unique genotypes, Table 2.). Population differentiation was also estimated without the isolated populations (12 and 13), showing that the contribution of these populations is negligible. Among the populations of the main area alone F_{st} for all trees was 0.295 and F_{st} for unique genotypes was 0.243. Between the two disjunct populations F_{st} was 0.104. The population structure seems to follow isolation-by-distance model within the core area as indicated by the statistically significant correlation between $F_{st}/(1-F_{st})$ and the logarithm of the geographic distance ($r=0.81$, $P=0.0003$), but the pattern was broken down, when the whole range was considered ($r=0.10$, $P=0.36$; Table 3, Fig. 2). Correlation was also significant within the main area ($r=0.29$, $P=0.03$) but the percentage of variation explained by the model was quite small (8.4%). This pattern is visualized in UPGMA dendrogram (Fig. 3), as populations of core area group into two small clusters and isolated populations join in without any geographic pattern. The logarithm of geographic distance had the same explanatory power as the plain distance (Table 3).

The number of recurring genotypes and their proportion in each population are presented in Table 4. In one population (nr 8) all of the genotypes were recurring when on an average 45% of the genotypes were recurring. However, few

Table 2. Averaged diversity within populations (H_s), total genetic diversity (H_t), average fixation index within populations (F_{is}) and genetic differentiation among populations (F_{st}) at 8 polymorphic loci. Overall diversity values are estimated using all loci. F_{st} is estimated according to Weir and Cockerham (1984), and the confidence limits (95%) are obtained by bootstrapping over the loci (Weir 1996). Separate estimates are shown for all samples (1st) and for unique genotypes only (2nd), separated by a slash.

Locus	H_s	H_t	F_{is}	F_{st}
Got2	0.396/0.421	0.495/0.500	–0.039/0.084	0.253/0.167
Idh	0.016/0.018	0.018/0.020	–0.123/–0.128	0.113/0.118
Aco	0.203/0.215	0.267/0.276	–0.008/0.052	0.254/0.277
Pgi2	0.433/0.452	0.502/0.503	–0.148/0.007	0.119/0.075
Pgd1	0.162/0.198	0.251/0.267	–0.088/–0.040	0.376/0.294
Pgm1	0.294/0.308	0.431/0.457	0.173/0.201	0.351/0.257
Fest3	0.089/0.105	0.097/0.110	0.026/–0.007	0.086/0.042
Sdh	0.168/0.194	0.340/0.350	–0.024/–0.046	0.524/0.438
Overall	0.088/0.096	0.120/0.124	–0.017/0.050	0.290/0.227
CL95 up	0.022	0.033	0.110/0.116	0.400/0.327
CL95 low	0.154	0.207	–0.105/–0.017	0.187/0.135

Table 3. Results of Mantel tests between $F_{st}/(1-F_{st})$ and geographic distance (plain and log-transformed) among all Finnish populations, main area (Kokemäenjoki rivershed) and core area (lake Vanajavesi).

Subset	distance			log(distance)		
	r	rxr%	P	r	rxr%	P
All Finnish	–0.04	0.2	0.80	0.10	1.06	0.36
Main	0.25	6.22	0.07	0.29	8.43	0.03
Core	0.83	68.78	0.0002	0.81	65.54	0.0003

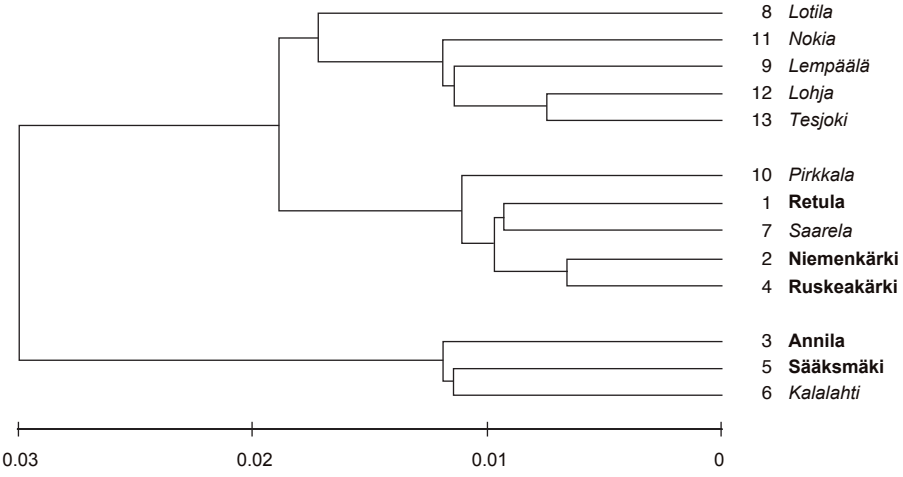

Fig. 2. UPGMA-dendrogram showing the genetic distances of the Finnish populations. Populations in the core area (Lake Vanajavesi) are shown in bold, others in italics.

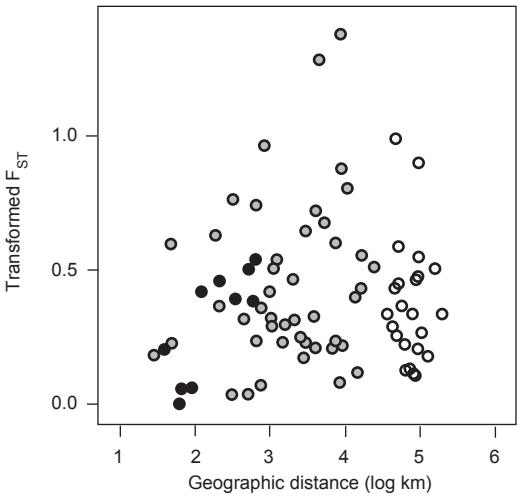

Fig. 3. Relationship between pairwise genetic (transformed F_{st}) and geographic distances (log-transformed) among Finnish populations of *U. laevis*. Solid circles represent pairs of populations within the core area, grey and solid circles together represent pairs within the main area (Kokemäenjoki watershed). Open circles represent pairs, where one or both of the populations is isolated.

Table 4. For each population, sample size (n) and statistics for all genotypes and individuals in recurring genotypes are given. Within genotypes, total number of different genotypes, number of recurring genotypes (Rec.) and number of genotypes with significantly low probability (<0.05) under sexual reproduction (Sign.) are shown. In the two last columns there are observed (Obs.) and expected (under sexual reproduction) (Exp.) numbers of individuals in recurring genotypes.

Population	n	Genotypes			Individuals in recurring	
		Total	Rec.	Sign.	Obs.	Exp.
1	25	15	7	1	17	5
2	32	21	6	0	17	7
3	44	37	6	1	13	3
4	14	9	3	0	7	2
5	24	14	5	0	15	8
6	39	9	8	1	38	27
7	51	30	14	2	35	11
8	39	7	7	1	39	29
9	44	33	9	5	20	1
10	47	21	8	0	34	15
11	54	21	11	0	44	13
12	48	26	9	0	31	19
13	21	10	4	0	16	5
Estonia	45	42	3	2	6	0

genotypes had significant probability for a second encounter and using Bonferroni correction, no significant probabilities were found. In all populations the actual number of trees representing a recurring genotype was higher than the expected number (Table 4). The basic genetic parameters did not change significantly when calculated with only unique genotypes, exception being the significantly negative values of F_{is}, which were closer zero and non significant (populations 8, 11 and 13; Table 1).

4 Discussion

4.1 Low Within-Population Variation and High Among-Population Differentiation in Marginal Populations of *U. laevis*

Finnish populations of *U. laevis* are significantly differentiated (F_{st}=0.290 for all trees and F_{st}=0.227 for unique genotypes) and harbor slightly reduced overall amount of neutral genetic diversity (H_e=0.088, H_t=0.120). The high differentiation is also found among the populations of the main distribution area (F_{st}=0.295 for all trees and F_{st}=0.243 for unique genotypes). Although very little is so far published on the patterns of genetic variation in *U. laevis* in general, there is indication that Finnish populations harbor less neutral genetic variation and populations within the country are more differentiated than populations in the central area of distribution (Machon et al. 1997). In this study, the amount of genetic diversity in the Estonian population (H_e=0.139) was higher than the mean of Finnish populations (H_e=0.088). Machon et al. (1997) found high level of isozyme variation in general in Northern French populations of *U. laevis* (H_t=0.231), and five of the six enzymes analyzed in that study

are included in our study. These results suggest that genetic diversity is reduced in the northern populations. The results from a European-wide microsatellite study (Whiteley 2004) are, however, partly different. In that study, marginal populations (Finland and southern France) were different from the populations in the Central Europe but the levels of expected heterozygosity were quite similar in central and northern European populations.

Species are expected to have highest abundance at the central areas of distribution with smaller and more disjunct populations at the margin areas of distribution (Brussard 1984). While the idea of central-marginal populations has been widely used in conservation biology, its genetic inference is still under debate. According to central-marginal hypothesis, genetic drift should affect more the smaller and more isolated marginal populations than less isolated and larger populations in the central area, and thus marginal populations should harbor less genetic variation and be more genetically differentiated than central populations. However, reviews of empirical studies have reported contradictory results on the patterns of distribution of genetic variation in marginal vs. central populations (Brussard 1984, Lesica and Allendorf 1995, Gaston 2003, Eckert et al. 2008). A case supporting the theory is *Fraxinus excelsior* with populations in southern Finland being much more differentiated ($F_{st}=0.123$; Höltken et al. 2003) than those in Southern Germany ($F_{st}=0.012$; Hebel et al. 2006). The high differentiation among marginal Finnish populations of *U. laevis*, probably a consequence of genetic drift, is also in concordance with the marginal-central hypothesis.

Whereas genetic drift causes differentiation between small populations, gene flow between populations counteracts the effects of drift, and according to the isolation-by distance model, degree of differentiation is expected to be positively correlated with geographic distance between populations (Slatkin 1993). Our results from the Mantel analyses indicate that the spatial structuring of the genetic diversity does not follow the same pattern throughout the Finnish distribution area. Within the core area (lake Vanajavesi), there is strong support for the isolation-by-distance structure, but this effect is broken down, when all populations are included in the analysis (Table 3, Fig. 3). This might be a consequence of the marginal location, where populations are small and therefore even fairly short distances create gaps in the gene flow.

4.2 Ecological Traits and Patterns of Genetic Variation

In general, differences in biology and ecology explain significant proportion of the species differences in within-population variation and between-population differentiation. Among tree species, broad-leaved trees generally have slightly higher differentiation between populations than conifers and population differentiation is generally lower in wind-pollinated than animal pollinated species (Hamrick et al. 1992). *U. laevis* is wind-pollinated tree with wind as the primary mean of seed dispersal and thus fairly high level of genetic diversity and low level of differentiation is expected. However, we found quite low expected heterozygosity ($H_e=0.08$) when compared to average for either wind-pollinated trees ($H_e=0.154$) or species with wind-dispersed seeds ($H_e=0.149$) in Hamrick's (1992) review. Also contrary to the expectation, our estimate for the population differentiation ($F_{st}=0.29$) is considerably higher than the averages in Hamrick et al. (1992), $G_{st}=0.077$ for wind-pollinated and $F_{st}=0.076$ for wind-dispersed species. Specifically, low levels of population differentiation have been reported for wind pollinated broadleaved tree species: for *Fagus sylvatica* $F_{st}=0.02$ (Konnert 1995), for *Quercus robur* $F_{st}=0.066$ (Vakkari et al. 2006) and for *Betula pendula* $F_{st}=0.032$ (Rusanen et al. 2003). The high differentiation in Finnish *U. laevis* populations is remarkable also considering the small distribution area, since the magnitude of observed differentiation is influenced by the geographic size of the sampled area if the populations follow isolation-by-distance rule (e.g. Kärkkäinen et al. 2004).

The amount and distribution of genetic variation may also be affected by clonal propagation, which is common phenomenon among some broad-leaved trees. Among European *Ulmus* species, taxa with high tendency of clonal propagation (e.g. *U. minor*; Gil et al. 2004) and with no clonal propagation (e.g. *U. glabra*, Goodall-Coperstake

et al. 2005) can be found. Role of clonal propagation in *U. laevis* seems to be rather restricted (Goodall-Coperstake et al. 2005). In this study we found high proportion of identical genotypes in some populations, but due to the low variability, they may as well be reproduced sexually. In any case, the high population differentiation is not a consequence of clonal propagation, as the differentiation estimate calculated using only the unique genotypes is still very high ($F_{st}=0.227$).

In many broad-leaved species, human impact can be seen in the genetic structure of populations. For example, some populations of *Populus nigra* were found to consist only of few clones planted by humans in river banks (Smulders et al. 2008) and English elm (*U. minor* var. *vulgaris*) has been found to originate from one clone brought to England by Romans (Gil et al. 2004). In Finland, elms have been planted in parks, but human impact on the riparian stands of *U. laevis* has been negligible.

Ecological characteristics of European white elm partly explain patterns of genetic variation. *U. laevis* is a riparian habitat specialist with limited and dispersed areas of suitable habitats. Riparian species may show slightly increased population differentiation, e.g. population differentiation in *Populus nigra* across European river systems was higher ($F_{st}=0.081$) than estimates from other *Populus* species with less specialized habitat requirements (Smulders et al. 2008). If flooding is irregular, habitat patches suitable for colonization are created only occasionally and the founder effect will be pronounced. In the case of Finnish *U. laevis*, the management of the lake Vanajavesi, starting in the 18th century and including several operations up to 1930's (e.g. see Vanajavesi), has decreased the water level and revealed new shoreline and may have been a driving force of colonization events lasting a few years at a time. Such fairly rare colonization events may have contributed to the observed high genetic differentiation.

4.3 Implications for Genetic Conservation

The conservation of marginal populations has been a controversial topic (Millar and Libby 1991, Lesica and Allendorf 1995, Hunter and Hutchinson 1994). Small marginal populations may suffer from detrimental effects of inbreeding and randomly lose genetic variation needed for adaptation to changing environmental conditions if populations are small and external gene flow very restricted. However, small populations may also genetically differentiate due to local selection and reduced gene flow between populations (Lenormand 2002, Kivimäki et al. 2007). Such marginal populations may be important during climate change, as they may become expansion centres which enable shift in species' geographical distribution (Safriel et al. 1994).

Finnish populations of *U. laevis* may have lost some degree of genetic variation, as indicated by fairly low expected heterozygosity in allozyme loci. On the other hand, there is no excess of observed frequency of homozygotes and thus no sign of increased inbreeding. For adaptive traits, Whiteley et al. (2003) estimated high heritabilities in many growth- and phenology related traits and showed significant differentiation between northern (Russia, Sweden) and southern (Germany, France) populations. In addition, Black-Samuelsson et al. (2003) found genetic differences between families in some additional traits related to growth and phenology and drought stress. In a related species, *U. glabra*, Myking and Skrøppa (2007) found also within-population variation and between-population differentiation in growth rate, bud burst and growth cessation, thus suggesting ample genetic variation in northern marginal populations in that species. Thus, very likely also Finnish populations of *U. laevis* harbour quite much adaptive genetic variation and the distribution of that variation should be studied. The high F_{st} in this study indicates prominent random drift, which may have influenced also adaptive traits.

Currently, material from 19 natural populations or small groups of *U. laevis* is growing in a dynamic ex situ collection, established under the national gene conservation programme (Suomen maa- ja metsätalouden… 2002). The total number of clones included so far is 121, 2–10 clones per population. When a collection was established, several grafts per clone were planted, but later on only one graft per clone will be left to participate in reproduction. The final aim is to both conserve genetic resources and produce seed with broader genetic base than is currently found in single populations.

For future conservation activities of *U. laevis*, there are two issues that should be considered. Firstly, the availability of suitable habitats should be guaranteed. Riparian species deserve special attention in conservation, and watershed management should be planned so, that the reproduction and even population expansion of *U. laevis* is possible. Assumed on the basis of Whiteley et al. (2003), the northern marginal populations possess suitable gene pool also for new colonizing populations. The other issue that has to be taken seriously in conservation activities is Dutch Elm Disease (DED). Detailed studies have shown that there is genetic variation in resistance against DED among Ulmus clones, and that variation was related to variation in phenology (Santini et al. 2005). Those results make northern populations with differentiated phenology very interesting study objects, especially when northernmost populations have not yet suffered from DED. Although European white elm has not suffered from DED as severely as some other elm species, it is susceptible to the disease (Solla et. al. 2005). Options to reduce risk of DED in the Finnish gene conservation program are 1) to plant a duplicate collection farther north, 2) to keep the grafts low (hedging) and 3) to use cryopreservation.

The distribution of variability within white elm in Finland is a challenge for gene conservation. Even within the core distribution area the level of genetic diversity varies notably from one stand to another, the range in H_e being from 0.050 to 0.123. Also, the change of IBD-structure has practical implications, e.g. the most remote populations are not genetically most unique. Still, in the light of this study it seems that the current approach for the genetic conservation of *U. laevis* in Finland is fairly well justified.

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