Morphological Intergradation of Native Elm Species Is Shown by Site-specific Parameters

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Abstract

As a consequence of the fragmentation and small size of populations caused by the destruction of their native habitats, elms are getting endangered in Lithuania. The aim of the study was to learn about the native elm species, *Ulmus glabra* Hudson and *Ulmus minor* Miller, and their hybrid, *Ulmus* × *hollandica* Mill., based on the research of site-specific parameters of canopy overlap, soil properties, and herb layer characteristics at the contact zones, where it may become increasingly difficult to differentiate pure forms from the hybrids. Conceivably, the morphological intergradation of native elm species can be related to the natural gradients of moisture, pH, and nutrients as well as North-South and up-down oriented parameters of canopy overlap of elms with surrounding woody species. Elm habitats were studied to establish a predictive model for the presence of the hybrids and species in the very few contact zones existing in Lithuania. Quick, Unbiased, Efficient Statistical Tree method (QUEST) was used to select predictors from the sixty eight site-specific parameters. In conclusion, the morphological intergradation of native elm species in the contact zones is shown by differences in soil type, canopy overlap and herbal cover.

Key words: *Ulmus minor*, *Ulmus glabra*, *Ulmus* × *hollandica*, morphological intergradation, soil type, herbal cover, canopy overlap, contact zone.

Introduction

The European Environment Agency report “Assessing Biodiversity in Europe – the 2010 report” highlights that the conservation status of species and habitats in Europe’s forests is bad. Even within the protected areas: 52% of species and 63% of habitats are in Unfavourable Conservation Status and only 21% are in Favourable Conservation Status. This indicates that current forest management practices albeit improving to some extent (e.g. increased amount of deadwood has been reported) have not been sufficient enough. The improvement of the pan-European forest management practices and standards for a better support of forest services by introducing a similar framework of Good Agricultural and Environmental Conditions to forestry is advocated as the conservation target for the development of a common forest legislative tool for Europe (BirdLife International 2012). The standards of “native tree species to station’s condition”, “mixed stands”, and “natural regeneration” are proposed to mitigate climate changes as well as to secure the survival of vital species populations, gene exchange and species movements. However, the presence of a species is not a guarantee for good habitat conditions. According to Tilman et al. (1994), a species population decline in response to habitat destruction occurs with a time delay, called the “extinction debt” (Lachat et al. 2013). But the worst of it is that ‘geographically restricted native species with sensitive requirements will continue to have high extinction rates while those widespread broadly tolerant forms that can live with humans, and benefit from their activities, will spread and become increasingly dominant’ (Brown 1989).

Native elms have not been investigated in Lithuania from bio-ecological and coenotic viewpoint and their role within forest ecosystem have not been evaluated yet. From the general characteristics, common to all Noble Hardwoods as defined by the EUFORGEN Network, it follows that strategies for the conservation and promotion of elms largely depend on site conditions – soil properties and the biotic and abiotic environment (Rotach 1999, Kriebitzsch et al. 2013). The novelty of the study was to determine site-specific parameters of canopy overlap indicative for the presence of elm hybrids. The aim of the study was to learn about the native elm species, the wych elm (*Ulmus glabra* Hudson), the field elm (*Ulmus minor* Miller), and their hybrid (*Ulmus × hollandica* Miller), based on the research of site-specific data at the contact zones, where morphological intergradation of elms occurs, and where it may become increasingly difficult to differentiate pure forms from the hybrids (Petrokas and Baliuckas 2012, Cox et al. 2012). Our hypothesis was that the hybrids inhabit different niches than those of the parental species (*U. glabra* and *U. minor*). Conceivably, the morphological intergradation of native elm species can be related to the natural gradients of moisture, pH, and nutrients, as well as North-South and up-down oriented parameters of canopy overlap of elms with surrounding woody species, which may refer even to the geomagnetic conditions of a site. For the roots of a plant contain starch molecules (protoplasm) that determine the effect of geomagnetism on plant. The alignment of roots is decided by the North and South poles of the Earth (Aarti 2009). The source of geomagnetism is an electrical current moving over the crust of the Earth toward the north magnetic field (Skow 1991). Soil pH reading is a measure to the speed of this current on its way to the north magnetic field. Wych elm's need for soil pH_{KCl} is 7.1-8.0; field elm's need is $pH_{KCl} > 8.0$ (Ellenberg et al. 1991).

The most generalised treatment of the complex taxonomical nature of European elms, at least in continental Europe, considers the presence of three species in this continent, the European white elm (*Ulmus laevis* Pallas), the wych elm, and the field elm (Richens 1983, Armstrong and Sell 1996). Therefore, the field elm, the wych elm, and the Dutch elm were taken as 'datum-taxa' in this study. Morphological differences within *Ulmus minor-Ulmus glabra* complex (Petrokas and Baliuckas 2012) are given in Table 1. In general, stem conformation and lobe angle at 25% of leaf blade height of Dutch elms (*Ulmus × hollandica* Miller) did not overlap with those of parent species (Petrokas and Baliuckas 2012). The Dutch elm is recognised also by bearing, particularly on root suckers and stool shoots, longitudinal periderm wings; the more vigorous the shoot, the deeper the wing (Elwes and Henry 1913, Smithson 1954). The wych elm (*Ulmus glabra* Hudson) has no corky wings on the twigs. It rarely produces root suckers differing in this respect from the Dutch elm and the smooth-leaved elm (Elwes and Henry 1913). The smooth-leaved elm (*Ulmus minor* ssp. *minor* Richens) is identified by corky ridges on young twigs. It is variable in the wild state in the amount of pubescence on the branchlets and leaves, and in the presence or absence of corky ridges on the twigs and branches (Elwes and Henry 1913). Smooth-leaved elm is the commonest type of the field elm in continental Europe today (Richens 1983, Mackenthun 2007).

Materials and Methods

Research into the differences in soil type, canopy overlap, and herbal cover has been started in the broad-leaved deciduous forests around the central part of Lithuania, distinguishable for its diversity of flora (Karazija 1988, Karazija and Vaičiūnas 2000, Rašo-

Table 1. Morphological differences within *Ulmus minor-Ulmus glabra* complex (Petrokas and Baliuckas 2012)

	Ulmus minor Miller	*Ulmus minor* ssp. *minor* Richens	*Ulmus × hollandica* Miller	*Ulmus glabra* Hudson
Suckering	Readily produces suckers from roots, even after devastation by Dutch elm disease	Suckers readily	Produces root suckers and stool shoots	Never produces root suckers
Corkiness	Young branchlets occasionally have corky wings	Variable in the presence or absence of corky ridges on the twigs and branches; in the cork-barked variety the branchlets are all corky	Longitudinal periderm wings on root suckers and stool shoots, most commonly four in number	No corky wings on the twigs
Leaf shape	Leaves unequal and often cordate at the base; acute, acuminate, or occasionally rounded at the apex	Mature leaves are smooth, glossy, bright green above, very unequal at the base, acuminate at the apex	Curly leaves without acute lobes, the base being very unequal	Leaves with few acuminate lobes at a broad apex, the base being strongly oblique with the lowermost lobe strongly overlapping, covering the petiole
Leaf margin	Biserrate	Biserrate	Leaf-teeth with a triple cerrulation	Biserrate, with both large and small teeth
Leaf nervation	No more than 8-11 (14) pairs of lateral nerves	About 12 pairs of lateral nerves, often forked	More than 14 pairs of lateral nerves, which are often forked up near the leaf-edges	15 to 18 (20) pairs of lateral nerves, which are often forked up near the leaf-edges
Pubescence	Leaves are dull, scabrous with scattered minute tubercles and minute hairs on the upper surface; lower surface densely pubescent with short hairs in spring, later glabrescent, but with conspicuous axil-tufts	Leaf stalk and shoot usually hairless at maturity; leaves are non-ciliate on the margins	Leaf-blades glabrous, and somewhat pubescent beneath	Stout densely villous petioles; leaves not ciliate on the margins, equally rough on the upper surface, though rather downy beneath

mavičius et al. 2001, Navasaitis et al. 2003). Descriptors for the site-specific parameters of elms are given in Table 2. The data on presumable hybrids were obtained from the very few existing contact zones of native elms at the Kunioniai, Šilas, Eleonoravas, Alovė, and Dūkštos (Table 3) during the mid-summer of 2012 and 2013. In total, the number of measured trees (valid cases, N) was 22: seven *U.* × *hollandica*, eight *U. glabra*, and seven *U. minor*. Lithuanian Forest Inventory data were used for selection of these sites. All the hybrids that were found were measured. The 'control' or pure species were selected close to these hybrids. Tree height was measured on standing tree by VERTEX IV device. Soil type is given in accordance with Karazija (1988) terminology.

The QUEST (Quick, Unbiased, Efficient Statistical Tree) method (Classification Tree procedure of SPSS 16.0 for Windows®) was used to select the predictors of the hybrids from the sixty eight parameters of canopy overlap, soil type, and herbal cover for use in building a formal model. For the QUEST method, the significance level for splitting nodes by default was

Table 2. Descriptors for the site-specific parameters in elm contact zones

Data	Descriptors	Parameters in total
Coordinates	Latitude, longitude, altitude	-
Tree species	1 – *Ulmus* × *hollandica*, 2 – *Ulmus glabra*, 3 – *Ulmus minor* Miller *sensu latissimo*	1
Tree measurements	Tree height (m) and crown projections (m) at the level of root neck at four cardinal directions, i.e. North/Northeast (NNE), North/Northwest (NNW), South/Southeast (SSE), South/Southwest (SSW)	1+4
Soil type	Soil moisture at elm sites by levels: N – normally moist, L – temporarily wet; soil fertility by levels: F – fertile, VF – very fertile, PF – particularly fertile; soil structure by levels: LR – light rocks, HR – heavy rocks, TR – light on heavy or twin rocks. The data is coded as 0 (not characteristic) or 1 (characteristic)	8
Canopy overlap	Overlap of crowns of elms with crowns of surrounding trees by species (including those of elms) along four cardinal directions: NNE, NNW, SSE, and SSW; tree heights in m are the values of the species, zero height value indicates no overlap	48
Herbal cover	Herb layer by height (< 0.5 or > 0.5 < 1.0 m) and density (scattered (< 5%), sparse (< 50%), full (100%), or gross (> 150%)) at the NNE, NNW, SSE, and SSW half-quarters from elm trees	4+4
Site condition	Current condition of canopy, undergrowth, underbrush, herbal cover, and soil at the NNE, NNW, SSE, and SSW half-quarters from elm trees by value: 0 – no disturbance (opening, trail, etc.), 1 – disturbed (rivulet, wind-slash, thinning, cutting, haul, etc.), 2 – violated (wind-throw, clearing, road, ditch, etc.)	4

Table 3. Locations and measurements of studied elms in elm contact zones

Location of contact zone	Tree[1] No.	Latitude	Longitude	Altitude, m	Tree height, m	Crown radius[2], m			
						NNE	NNW	SSE	SSW
Kunioniai	107	55°12’48.0’’	23°47’44.8’’	55	21.0	3	3	2	2.5
	259	55°12’37.5’’	23°47’44.4’’	54	9.5	1.5	2	1	1.5
	109	55°12’50.1’’	23°47’47.6’’	57	13.5	2	1.5	2	2.5
	369	55°10’56.7’’	23°46’10.2’	58	13.6	2	2.5	3	3
	270	55°10’58.3’’	23°46’07.5’’	58	12.5	1.5	3	2	2
Šilas	260	55°15’09.2’’	24°15’11.5’	27	10.5	2	2.5	2	2
	356	55°15’03.0’’	24°15’25.0’’	64	9.0	2	3	1	2
	361	55°14’13.9’’	24°17’45.8’’	72	5.0	1.5	1	1	2
Eleonoravas	152	55°09’56.7’’	23°03’07.0’’	64	28.5	0	2.5	3	3.5
	151	55°09’57.7’’	23°03’06.9’’	64	22.0	2	3	2	2.5
	267	55°09’58.6’’	23°03’09.5’’	62	18.5	2	4.5	2	3.5
	368	55°09’58.1’’	23°03’13.8’’	62	22.9	2	3	2	2
Alovė	364	54°21’30.3’’	24°08’54.6’’	120	13.2	3	2	2	3
	265	54°21’30.5’’	24°08’53.7’’	125	21.3	4	5	5	4
	266	54°21’30.5’’	24°08’53.7’’	125	15.2	2	2.5	2	3
Dūkštos	135	54°50’00.8’’	24°57’43.1’’	132	10.5	2	1.5	1	2
	157	54°50’06.7’’	24°57’32.8’’	135	13.3	1	1.5	1.5	1
	158	54°50’06.7’’	24°57’32.8’’	135	8.6	1	2	1	1
	371	54°50’06.5’’	24°57’34.7’’	135	17.7	2	3	3	3
	272	54°50’01.2’	24°57’41.7’’	134	8.7	3	3	3	3
	273	54°50’03.2’’	24°57’36.3’’	135	21.0	3	3	3	3
	374	54°50’03.9’’	24°57’28.3’’	134	12.2	2	1.5	2	1

[1] The first digit, reading from left to right, means species of elm (*Ulmus* spp.): 1 – *U.* × *hollandica,* 2 – *U. glabra,* 3 – *U. minor.* The rest two digits stand for sequential number

[2] Along four cardinal directions: NNE – North/Northeast, NNW – North/Northwest, SSE – South/Southeast, SSW – South/Southwest

0.05. Tree-based classification model classified cases into groups or predicted values of dependent (target) variable based on values of univariate independent (predictor or explanatory) variables. The influence of two elm categories (i.e. hybrids or species) of predictor variables (i.e. site-specific parameters) to the dispersion of residuals was checked using Levene's test for equality of variances. If the resulting *P*-value of Levene's test was less than 0.001, the obtained differences in sample variances were unlikely to have occurred based on random sampling from a population with equal variances.

Classification tree model summary for the presence of elm categories shown by site-specific parameters is given in Table 4. The Specifications section provides information on the settings used to generate tree model, including the variables used in the analysis. The Results section displays information on the number of total and terminal nodes, depth of the tree (number of levels below the root node), and independent variables included in the final model. The terminal nodes—nodes at which the tree stops growing—represent the best classification predictions for the model. To validate a classification tree Cross-Validation method was applied. Index was the ratio of the response percentage for the 'hybrids' target category compared to the response percentage for the entire sample. The index value was basically an indication of how far the *observed* target category percentage for that node differed from the *expected* percentage for the target category. The target category percentage in the root node represented the expected percentage before the effects of any of the independent variables were considered. An index value of greater than 100% meant that there are more cases in the target category than the overall percentage in the target category.

Data set of seventy three variables was then used to perform SAS MODECLUST procedure (SAS Institute, Inc., SAS/STAT$^{®}$ 9.2) and to produce density estimates and cluster membership for 22 elm trees. This procedure clustered elms in the data set by using the method six (METHOD=6), which is related to a method invented by Koontz and Fukunaga (1972a) and discussed by Koontz and Fukunaga (1972b). Option R=125 specified the radius of the sphere of support for uniform-kernel density estimation and the neighborhood for clustering.

Results

The estimation of statistical relationships between elm categories (i.e. hybrids or species) and soil structure or canopy overlap of elm trees with surrounding trees was not possible as the categories had different amounts of variability between the scores, i.e. the resulting *P*-values of Levene's test were less than 0.001 (Figure 1 and 2). Therefore, the null hypothesis of equal variances was rejected and it was concluded that there was a difference between the variances in the population.

One independent (predictor) variable was specified and included in the final model for the presence of elm categories shown by soil fertility of elm sites (Table 4). Tree diagram (Figure 3) shows that using the QUEST method, 'fertile soil' (SoilF) is the best predictor of elm categories. The "predicted" category for node 1 is 'species'. 36.8% cases of zero category of SoilF ('non-fertile soil') were hybrids. Index value

Table 4. Classification tree model summary for the presence of elm target categories (i.e. hybrids or species) shown by site-specific parameters. Variables included in the final models are in **bold**

		Soil structure	Canopy overlap	Soil fertility	Herbal cover
Specifications	Independent Variables	HR, LR, TR*	NNE_Asp, NNE_Oak, NNE_Bir, NNE_Lin, NNE_Hor, NNE_BAl, NNE_FE, NNE_Spr, NNE_HE, NNE_ha, NNE_ro, NNE_ab, NNE_bc, NNW_Asp, NNW_Oak, NNW_Bir, NNW_Map, NNW_BAl, NNW_Spr, NNW_WE, NNW_FE, NNW_HE, NNW_ha, NNW_ro, NNW_es, NNW_bc	F, VF, PF	HeightNNE, HeightNNW
	Maximum Tree Depth	5	5	5	5
	Minimum Cases in Parent Node	6	6	6	6
	Minimum Cases in Child Node	3	3	3	3
Results	Independent Variables Included	**HR**, **LR**, TR	**NNW_Bir**, NNE_Asp, NNE_ro, NNW_Spr, NNW_es	**F**	**HeightNNE**, HeightNNW
	Number of Nodes	5	3	3	3
	Number of Terminal Nodes	3	2	2	2
	Depth	2	1	1	1

* Abbreviations: Soil type: fertility: F – fertile, VF – very fertile, PF – particularly fertile; structure: HR – heavy, LR – light, TR – light on heavy or twin rocks. Direction: NNE – North/Northeast, NNW – North/Northwest. Tree species: Asp – aspen, BAl – black alder, Bir – birch, FE – field elm, HE – hybrid elm, Hor – hornbeam, Lin – linden, Map – maple, Oak – oak, Spr – spruce, WE – wych elm, ab – alder buckthorn, bc – bird cherry, es – European spindle, ha – hazel, ro – rowan

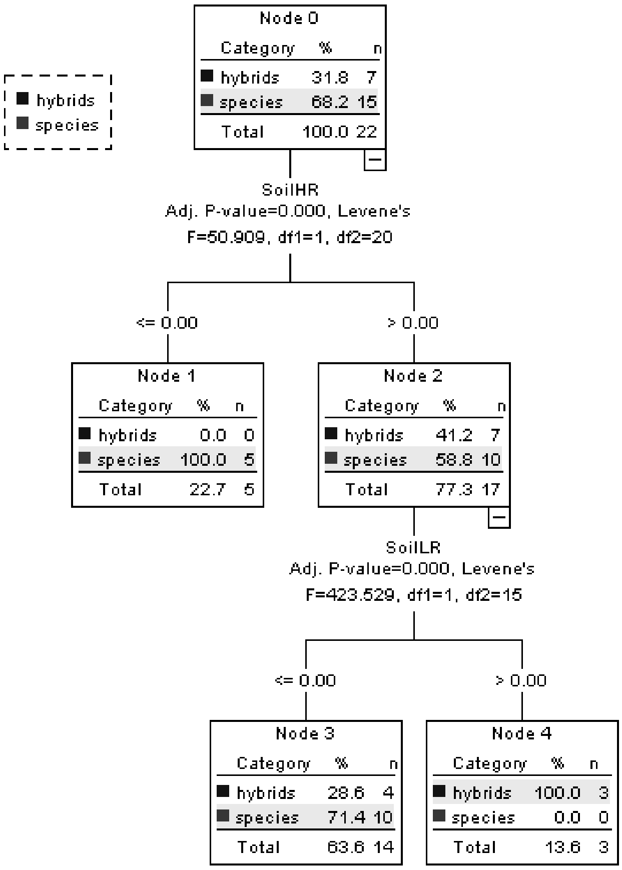

Figure 1. Graphic representation of the tree-based classification model for the presence of elm categories (i.e. hybrids or species) shown by soil structure (SoilHR – 'heavy rocks', SoilLR – 'light rocks') of sites. The model classifies cases into predicted values of dependent variable (i.e. hybrids or species) based on values of independent variable (i.e. heavy rocks or light rocks; the data is coded as 0 – not characteristic, or > 0 – characteristic). The influence of two elm categories of soil structure to the dispersion of residuals is checked using Levene's test

for node 1 was 115.8%. It means there were more cases in the 'hybrids' target category than the overall percentage in 'hybrids' target category. The model classified approximately 68.2% of elms correctly.

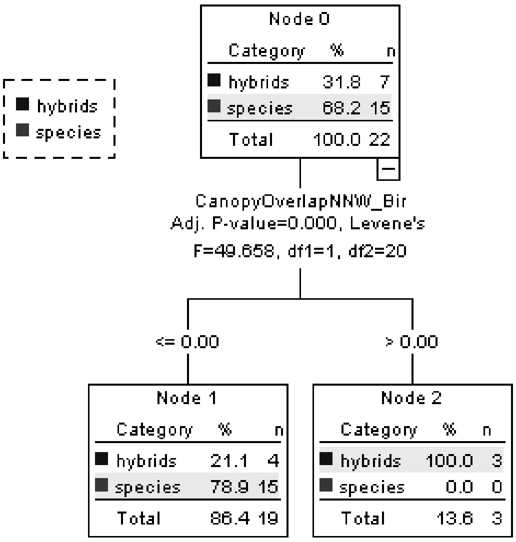

Figure 2. Graphic representation of tree-based classification model for the presence of elm categories (i.e. hybrids or species) shown by the overlap of canopy of elm trees with surrounding trees (Bir – birches) by heights (zero height value indicates no overlap) along the North/Northwest (NNW) direction from elm trees

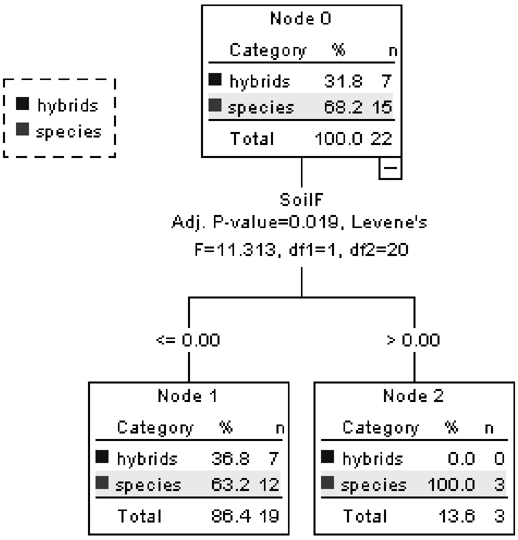

Figure 3. Graphic representation of the tree-based classification model for the presence of elm categories (i.e. hybrids or species) shown by soil fertility (SoilF - 'fertile soil'; the data is coded as 0 - not characteristic, or > 0 - characteristic) of elm sites

Two independent (predictor) variables were specified but only one was included in the final model for the presence of elm categories shown by herbal cover height at elm sites (Table 4). Tree diagram (Figure 4) shows that using the QUEST method, herbal cover height along the North/Northeast direction from elm trees (HerbalCoverHeightNNE) was the best predictor of the hybrid presence at elm contact zones. 36.8% cases of category 0.5 of HerbalCoverHeightNNE (i.e. herbal cover height of > 0.5 < 1.0 m) were elm hybrids. Index value for node 1 was 115.8%. It means there were more cases in the target category than the overall percentage in the target category. The model classified approximately 68.2% of the elm trees correctly.

In general, elm hybrids were found at the dryer sites of wet and very fertile forest patches (Table 5).

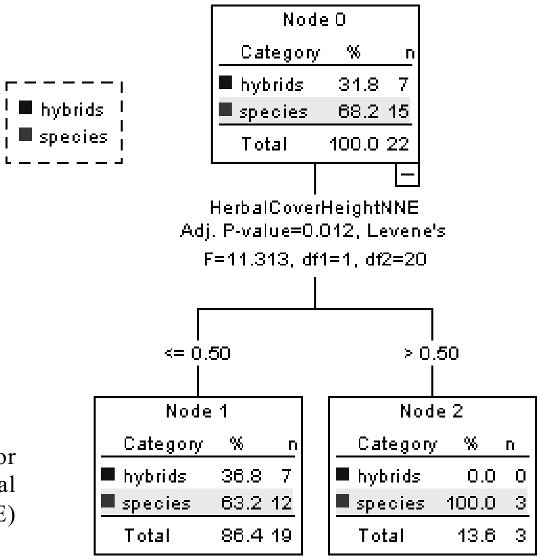

Figure 4. Graphic representation of tree-based classification model for the presence of elm categories (i.e. hybrids or species) shown by herbal cover height (< 0.5 or > 0.5 < 1.0 m) along the North/Northeast (NNE) direction from elm trees

Table 5. Summary data on elm contact zones. Atypical cases are in **bold**

Forest[1] (NATURA 2000 Code)	Species surrounding elms (number of trees)	Soil type[2]	Tree[3] No.	Cluster[4]
Kunioniai (9020)	Aspen – *Populus tremula* (3) Birch – *Betula pendula, B. pubescens* (2) Spruce – *Picea abies* (2) Oak – *Quercus robur* (1) Ash – *Fraxinus excelsior* (1) Hazel – *Corylus avellana* (1)	Lfs	107	1
		Lds	259	1
			109	1
			369	2
			270	2
Šilas (9020)	Oak – *Quercus robur* (2) Maple – *Acer platanoides* (2) Hazel – *Corylus avellana* (2)	Lds	361	1
		Ndp	260	1
			356	1
Eleonoravas (9020)	Linden – *Tilia cordata* (4) Birch – *Betula pendula, B. pubescens* (3) Black alder – *Alnus glutinosa* (3) Aspen – *Populus tremula* (2)	Lds	152	1
			151	1
		Lfs	267	1
			368	1
Alovė (91E0)	Black alder – *Alnus glutinosa* (6)	Lcl	364	1
			265	2
			266	2
Dūkštos (9020)	Aspen – *Populus tremula* (8) Oak – *Quercus robur* (3) Sallow – *Salix caprea* (1)	Lds	272	2
			157	2
			158	2
		Nds	273	2
			374	2
			135	**3**
			371	**4**

[1] 9020 – Fennoscandian hemiboreal natural old broad-leaved deciduous forests rich in epiphytes, 91E0 – Alluvial forests (Raðomavièius et al. 2001)
[2] N – normally moist, L – temporarily wet, c – fertile, d – very fertile, f – particularly fertile, l – light, s – heavy, p – light on heavy or twin rocks (Karazija 1988)
[3] The first digit, reading from left to right, means species of elm (*Ulmus* spp.): 1 – *U.* × *hollandica*, 2 – *U. glabra*, 3 – *U. minor*. The rest two digits stand for sequential number
[4] SAS MODECLUS (METHOD=6, R=125) cluster membership for the elms

Contrary to the elm species they grew together with birches (Table 6). Tree diagram (Figure 2) shows that canopy overlap of elms with birches along the North/Northwest direction from elm trees (CanopyOverlap NNW_Bir) indicates elm hybrids in the category of non-zero value.

Discussion and Conclusions

As a consequence of the fragmentation and small size of populations caused by the destruction of their native habitats, elms are getting endangered in Lithuania. Relics of former natural ecosystems, the elm trees, become transferred beyond their native habitats due to the shift from naturally-disturbed to managed forests. Clear-cuts, road verges, drainage ditches, power line rights-of-way serve as examples of forest openings at elm contact zones in Lithuania. They are subjected to the human-induced disturbance regimes of managed forests. As traditionally practiced, existing silvicultural systems do not incorporate landscape- and stand-level complexity characteristic of natural disturbance regimes (see Lindenmayer and Franklin 2002), thus the landscape and stand-level approaches are to be taken to address issues related to the maintenance of native elm species known to be closely associated with late-successional forests. Two main

Table 6. Summary for the canopy overlap of elms with surrounding trees by species and numbers at the North/Northeast (NNE), North/Northwest (NNW), South/Southeast (SSE), and South/Southwest (SSW) half-quarters from elm trees

Elm target categories (number of trees)	Half-quarters	Aspen	Black alder	Birch	Oak	Linden	Maple	Ash	Spruce	Hazel	Sallow
Hybrids (7)	NNE/NNW*	2		2	1	1			1		
	SSE/SSW	3	1	2	1						
Species (15)	NNE/NNW	4	4	1	3	2	1		1	1	
	SSE/SSW	4	4		1	1	1	1		2	1

natural forest disturbance regimes are characteristic for moist and wet forests where native elms live: (1) succession after stand-replacing disturbance from young forest to old-growth with shade-intolerant species in the beginning and shade tolerant species later on, and (2) gap dynamics (Angelstam and Kuuluvainen 2004).

The process of morphological intergradation of native elm species in the contact zones is shown by site-specific properties of soil (i.e. 'fertile soil'; Figure 3) and herbal cover (i.e. herbal cover height along the North/Northeast direction from elm trees; Figure 4). This occurs at non-riparian habitats, as in riparian habitats the reproductive system of field elm may exist in a dynamic equilibrium between periodic sexual reproduction following flooding and clonal proliferation during the intervening years when seedling establishment is not favoured (see Lopez-Almansa et al. 2003). This is seen from Table 6, as black alder, an early successional tree species, was found mainly at elm species' sites. While the black alder likes marshy, wet soil, wych elm finds it very difficult to grow in very wet, flooded areas. Wych elm thrives on moist rich forest slopes and in groves along streams (Gabrilavičius et al. 2013). In ash, oak, linden, and aspen forests it grows disseminated; mature ash stands are remarkable for the largest growing stock volume of wych elm in Lithuania (Petrokas 2011). In contrast to wych elm, the typical habitat of field elm is low-lying forest along the main rivers, growing in association with oak and ash, where it tolerates summer floods as well as droughts (Heybroek et al. 2009). Elm hybrids were found growing together with early successional shade-intolerant birches at the poorer sites of periodically wet broad-leaved deciduous forests (see Table 5, 6, and Figure 3).

It is crucial to realize the importance of individual variation within *Ulmus minor-Ulmus glabra* complex, because each individual tree has its own unique record of life-history exposures and experiences (Kültz et al. 2013), which may refer even to soil magnetism, for example. Natural elm hybrids are distinguished by tree-like conformation (i.e. excurrent main axis; Petrokas and Baliuckas 2012); they were found at the periodically wet (hydromorphic) sites. Is this connected with soil magnetism? It is known that the minimal values of soil magnetism are specific for hydromorphic sites of landscapes (Menshov and Sukhorada 2010). It is also known, that any types of energy like an inverse-electromagnetic current of many amperes flowing through free space without any electrons all make these tree-like patterns such as a stream flowing down the side of a mountain or fresh water percolating up through the sand on a beach. On the other hand, there exist places on the Earth where magnetic field assumes the form of a circular shape that exhibits upward and downward motion, during which monitoring equipment detects no North-South polarity (Lonetree 2010). This can indicate an anomalous electromagnetic activity causing trees to grow in gnarled and twisted patterns, to adopt a serpentine or spiral-like conformation. The most magnetic types of soils, such as chernozems, grey forest soils, chestnut soils, can be the main source of anomalous magnetic field, if soils superpose low-magnetic rocks (Menshov and Sukhorada 2010).

Hybridization is an important mechanism for producing "evolutionary novelty" and is considered to be a common mode of speciation in plants (Abbott 1992, Futuyma 1998). It can have net negative effects on biodiversity via speciation reversal, but on the other hand it may rescue native biota from looming extinction (Seehausen et al. 2008). The hybrids may be better adapted to the intermediate conditions present at an ecotone (i.e. the transitional zone between two vegetation communities), and may persist, increasing species richness (Senft 2009). This has been shown to occur in a few isolated cases such as hybrids between *Iris fulva* and *I. hexagona* (Arnold 1994), between two subspecies of *Artemesia tridentata* (Wang et al. 1997), and between *Eucalyptus melanophloia* and *E. crebra* (Drake 1980). Our data indicates ecotonal differences in early successional tree species surrounding elms: the hybrids were found growing together with shade-intolerant birches, while black alders were present mainly at parental species' sites (Figure 2, Table 6). Our data also shows some differences in herbal cover. However, an ecotone for one group of species (e.g., trees) may not be an ecotone for other groups (e.g., herbs). It could be interesting to increase sample size of the pure elm species in future studies, in order to determine better their ecological niches.

Study described here tried to explain the role of site-specific parameters in choice of elms spot to be considered retained. Findings of atypical cases (see Table 4) suggest that elm contact zone with its surroundings in the Dūkštos forest needs to be delineated as a key habitat. We suggest minimum size for set-aside patch > 1 ha (see Müller et al. 2012). The reason it should be excluded from any use is that more widely distributed refugia are needed for forest organisms with limited dispersal capabilities (Lindenmayer and Franklin 2002). Moreover, maintenance of habitat across multiple scales must be the overarching objective of plans for native elm conservation if they are to be effective. We also propose that the process of forest management for native tree species' maintenance should refer to the organism-specific concept of habitat (see Whittaker et al. 1973). Hypothetically, it's necessary to investigate effects of hybridization identifying organismal traits across habitat scales (see Franklin et al. 1986, Lewontin 2000, Tagliapietra and Sigovini 2010, Bollmann and Braunisch 2013, Kriebitzsch et al. 2013). "The organism is the central unit for integration of both of the major determinants of biological form and function—genes and the environment" (Lewontin 2000 cited in Kültz et al. 2013).

In the study we tried to determine what the microhabitat conditions are where Dutch elm (*U.* × *hollandica*) grows. The results shed light on the microhabitat conditions that are required by the parental species and Dutch elm, which can potentially be useful for forest managers and the conservation of these species. Our data also shows the importance of soil properties in species distribution and their ecology. It is important to stress, however, that the sample size was small (22 individuals, of which seven were hybrids) and, therefore, cautions were taken before generalising the results of the study. Furthermore, to understand the significance of evidence for interspecific hybridization and emergence of a hybrid swarm within *Ulmus minor-Ulmus glabra* complex additional tests are required, including: (1) statistical tests to discriminate between real and spurious discordance resulting from poor data; (2) historical population genetic studies to discriminate between hybridization and ancestral polymorphism; (3) experimental studies to investigate effects of hybridization on functional diversity; and (4) quantitative tests of biogeographical predictions (Seehausen 2004).

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МОРФОЛОГИЧЕСКАЯ ИНТЕРГРАДАЦИЯ МЕСТНЫХ ВИДОВ ВЯЗА ПОКАЗАНА САЙТ-СПЕЦИФИЧЕСКИМИ ПАРАМЕТРАМИ

Р. Петрокас и В. Балюцкас

Резюме

Как следствие фрагментации и немногочисленности популяций, обусловленных уменьшением благоприятной среды произрастания, вязы в Литве находятся под угрозой вымирания. В данном исследовании видоспецифические свойства родительских видов вяза – *Ulmus minor* и *Ulmus glabra* – и их гибридов – *Ulmus* × *hollandica* – определены на основе анализа сайт-специфических параметров перекрытия крон, свойств почвы, характеристик травяного покрова в контактных зонах, где различия между чистыми видами и гибридами становятся менее чёткими. Предположительно, морфологическая интерградация обоих видов может быть связана с естественными градиентами влажности, pH и питательных веществ, а также с параметрами перекрытия крон вязов и расположением в непосредственной близости растущих древесных видов (север-юг, верх-низ). В целом, места произрастания вязов изучались таким образом, чтобы установить прогностическую модель на наличие гибридов и видов в очень немногочисленных контактных зонах, существующих в Литве. Чтобы выбрать прогностические параметры из шестидесяти восьми сайт-специфических параметров, был использован метод под названием Быстрое, Несмещенное, Эффективное Статистическое Дерево (Quick, Unbiased, Efficient Statistical Tree, QUEST). По данным исследования контактных зон, морфологическую интерградацию местных видов вяза показывают различия в свойствах почвы, перекрытии крон и травяном покрове.

Ключевые слова: *Ulmus minor*, *Ulmus glabra*, *Ulmus* × *hollandica*, морфологическая интерградация, тип почвы, травяной покров, перекрытие крон, контактная зона.