

Understory changes in mixed elm stands in response to canopy dieback in Latvia

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Abstract

In the eastern Baltic region, warming is favouring the advance of thermophilic tree species and the formation of mixed stands with a higher share of broadleaves, thus contributing to productivity and other ecosystem services of forests. However, the accelerating environmental changes often trigger the spread and intensification of biotic disturbances such as disease outbreaks at unprecedented rates, which might alter the course of stand development. Within the region, elms *Ulmus* sp., which are of low importance as a source of timber, yet highly important in terms of other ecosystem services, are suffering varying degree of dieback due to the Dutch elm disease, which can threaten the existence of species. Still, there are explicit local differences in the susceptibility of trees, which add uncertainties regarding the sustainability of elms. A permanent sampling plot network was established to monitor changes in mixed elms stands in response to the dieback caused by the disease; canopy and understory trees were accounted. Two surveys in 2016 and 2021 have been made. Canopy elms have suffered moderate dieback during the first wave already before the surveys, as ca. 17% of canopy elms were already dead. However, the susceptibility differed among the species (*Ulmus glabra* exceeded *U. laevis*), likely due to the preference of the vectors of the disease. In response to canopy openings, self-regeneration occurred, though the balance between the advance regeneration and undergrowth species was affected by the intensity of canopy dieback. The advanced growth of the former canopy species including elms was sufficient under moderate changes in the canopy, while low and high changes favoured undergrowth, suggesting the formation of shrubland. Accordingly, the additional mortality of elms due to Dutch elm disease tended to diverge the development course of the mixed broadleaved stands; hence further monitoring is advised.

Keywords: *Ulmus* sp.; *Ophiostoma* sp.; advance growth; undergrowth; Dutch elm disease; succession

Introduction

In the eastern Baltic region, climatic changes are causing the expansion of thermophilic deciduous (broadleaved) tree species, as well as increasing forest productivity (Kellomäki et al. 2018, Torresan et al. 2020, Socha et al. 2021), which, however, is becoming sensitive to water shortage (Allen et al. 2015). Simultaneously, climatic changes facilitate the introduction/spread of pests and diseases, opposing the projected increase in productivity (Kowalski 2006, Canelles et al. 2021, Panzavolta et al. 2021, Tkaczyk 2022). However, such interactions are complex, particularly due to the legacy effects of intensifying disturbances (Seidl et al. 2017, Sierota et al. 2019), which can change the pest-host interactions (Linnakoski et al. 2019), leading to disproportional consequences (Venäläinen et al. 2020, Panzavolta et al. 2021). Accordingly, assessing the pest-host interaction for local populations and its effect on the course of stand development is crucial for adaptive and close-to-nature forest management (Linnakoski et al. 2019).

Wych Elm *Ulmus glabra* Huds. and European white elm *U. laevis* Pall. (besides field elm *U. minor* Mill., which is absent in the Baltics) are widespread broadleaved tree species in Central and Western Europe, as well as northwards up to the mid-part of the eastern Baltic region (Saarse and Veski 2001, Collin 2003). Elms are of intermediate to low commercial interest (Collin 2003); however, they are important ecologically (Jürisoo et al. 2019) due to a high number of associated species and habitats, as well as ecosystem services provided (Jüriado et al. 2009, Thor et al. 2010, Moricca et al. 2018, Marčiulynas et al. 2022). Thus, elms contribute to ecosystem functioning and sustainability of forests across diverse landscapes (Petrokas and Baliuckas 2014, Caudullo and De Rigo 2016, Marčiulynas et al. 2022).

Since the early 20th century, Dutch elm disease (DED) – a lethal wilting and dieback of native elm species *Ulmus* sp. – has been spreading throughout North America and Europe (Brasier 1990). Three fungal pathogens cause the disease, the less virulent *Ophiostoma ulmi*

(Buisman) Nannf., and highly virulent *O. novo-ulmi* Brasier and *O. himal-ulmi* Brasier et Mehrotra (Brasier 1991, Brasier and Mehrotra 1995), which are distributed by elm bark beetles *Scolytus* sp. (Ploetz et al. 2013, Menkis et al. 2016, Webber 2020), and locally via root contacts (Santini and Faccoli 2015). Due to highly mobile vectors, management of the DED has been largely unsuccessful (Harwood et al. 2011). Accordingly, the invasion has turned into a pandemic (Brasier and Kirk 2001) threatening elms (Litkowiec et al. 2022) and reducing their populations (Brasier 2000), thus altering biotic relationships and hence functioning of temperate mixed forests (Brasier and Kirk 2001).

Elms show signs of effective self-regeneration (Collin 2003); however, their saplings and advance growth suffer from DED struggle competition with undergrowth, implying advancing changes in stand composition (Harwood et al. 2011). Hence natural succession of elm stands can be altered towards developing a shrubland (Givnish 2002, Royo and Carson 2006). However, the severity of DED varies regionally (Solheim et al. 2011, Jürisoo et al. 2019, Czeszczewik et al. 2022), suggesting uneven potential for elms to survive the struggle. For instance, in Latvia, DED was confirmed only in 2020, presuming some resilience of elms (Matisone et al. 2020). Under such conditions, communities of regenerating trees (advanced growth) are indicative of the development of the affected stands, acting as a model for the adaptability and sustainability of broadleaved stands (Czeszczewik et al. 2022).

The study aimed to assess the changes in understory composition in affected *Ulmus* sp. stands in hemiboreal mixed broadleaved stands in Latvia and to evaluate potential transformations. We hypothesized that the regeneration of elms in previously elm-dominated stands has decreased due to DED causing their substitution by other shade-tolerant broadleaves.

Methods

Studied sites, sampling, and measurements

The study was based on a network of 18 permanent sample plots (PSPs) in Latvia (Figure 1). The PSPs were established in 2015/2016 to monitor maturing/mature un-

even-aged mixed deciduous stands (time since clear-cut 56–143 years) irrespectively of the management history (Supplementary 1). These stands were selected (by stratification) from the national forest inventory and had high admixture (> 40%) or were dominated by elms, which have been subjected to a varying degree of DED. There was also an admixture of common ash *Fraxinus excelsior* L. in a few stands, which has suffered dieback (Matisone et al. 2018, Supplementary 2). A single circular plot ($r = 15$ m, $S \sim 706$ m²) per stand was established. The sampled stands (0.5–6.3 ha) grew on flat terrain on mesotrophic and eutrophic freely-draining mineral or drained forest soil, though in a few plots (Kemerī, Verēne, and Aināzi), periodical (spring) waterlogging occurred (Supplementary 1).

The climate in the study region was temperate moist continental, with the mean annual temperature (\pm standard error) in the western and eastern parts of Latvia of 7.0 ± 1.4 and $6.1 \pm 1.6^\circ\text{C}$, respectively; January was the coldest (-1.8 ± 0.7 and $-4.5 \pm 1.0^\circ\text{C}$, respectively) and July was the warmest (17.4 ± 0.3 and $17.9 \pm 0.3^\circ\text{C}$, respectively) month according to the data from Harris et al. (2020). The mean annual precipitation was 706 ± 67 mm; the highest monthly precipitation occurred during the summer months (June–September; 72 ± 29 mm/month). The vegetation period (mean diurnal temperature $> 5^\circ\text{C}$) lasted from mid-April to October and has extended by ca. 10 days during the last century.

All trees, including deadwood, within each PSP, with a stem diameter at breast height (DBH) ≥ 6 cm were measured. For each tree and log/snag, DBH and height/length (H) were recorded with an accuracy of one and 50 cm, respectively. Generally, a sampling technique according to Matisone et al. (2018) was used. Within each plot, three smaller circular sub-plots with a total area of 235.6 m² were placed in three directions (0° , 120° , 240°) at a distance of seven metres from the centre to account for understory. In each of these sub-plots, the height of all advance growth trees/saplings (AG) and undergrowth/shrub (UG) individuals with a height > 10 cm and DBH < 6 cm was recorded with a precision of 50 cm (according to 50 cm height classes, as the individuals were numerous and ground cover vegetation was scarce). The surveys were repeated in 2020/2021.

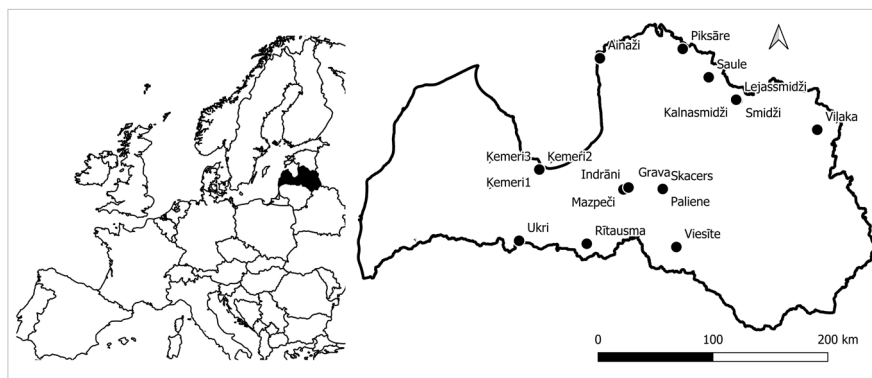


Figure 1. Location of the studied permanent sample plots of broadleaved stands

Data analysis

For the description of overstory (canopy and sub-canopy trees with DBH > 6 cm) in each plot, density and standing stock (living and standing deadwood) were calculated based on the local equation. The volume of lying deadwood was calculated as for a truncated cone. The proportion of each canopy species (regarding standing stock) was calculated to describe stand composition. To assess the mortality of *Ulmus* sp. and other canopy species during the analysed period, the mortality rate, $r\%$, was calculated:

$$r\% = \frac{N_1 - N_{1+t}}{tN_1}, \quad (1)$$

where N_1 is the number of trees at the beginning of the observation period, N_{1+t} is the number of trees at the end of the observation period, and t is the length of the observation period, in years.

Species richness, occurrence, the Shannon-Wiener diversity index (H'), Ellenberg's indicator values (L – light, F – moisture, T – temperature, C – continentality, R – reaction, N – soil richness) for AG and UG were calculated for the indirect description of undergrowth and site conditions (Ellenberg et al. 1991). The understory composition changes among the observation periods were compared using the ANOSIM (Analysis of Similarities). The relationships between the understory characteristics of plots, as well as AG and UG density separately, and the density of living and dead canopy elms were assessed by a simple linear model. A similar approach was also used to assess the relationships between the height of AG and UG.

The Detrended Correspondence Analysis (DCA, detrending with 26 segments and downweighing rare species), based on the understory species abundance (density), was employed to assess the successional changes in the understory composition of stands between the surveys. A randomization test with 1,000 iterations was performed to determine the significance of DCA components. To assess the relationships of the two main ecological gradients of the understory composition (as represented by the DCA scores) with tree stand (canopy) properties and the indirect indicators of site properties represented by Ellenberg's indicator values, linear mixed regression analysis (with sample plot included as the random effect to generalize across the surveys) was used. The sets of predictors were selected arbitrarily based on the correlations with the principal gradients and tested for collinearity. Compliance with the statistical assumptions was checked by the diagnostic plots. The data were analysed in R v. 4.2.2 (R Core Team 2022), using the software packages “lme4” (Bates et al. 2015) and “vegan” (Oksanen et al. 2022) at the significance level of $\alpha = 0.05$.

Results

In the studied stands/plots, a total of 12 canopy tree species was accounted; however, the number of canopy species per plot ranged from three to seven indicating mod-

erate richness and compositional diversity. In both surveys in the studied stands, the highest density (> 130 trees ha⁻¹) was observed for *U. laevis*, *U. glabra*, and black alder *Alnus glutinosa* (L.) Gaertn., but the highest occurrence was for *U. glabra*, *U. laevis*, and *F. excelsior* (Table 1) according to the selection criteria of the stands. Still, the occurrence of elms indicated the abundance of hosts for DED in the studied stands, suggesting the initial stage of the disease.

The density of canopy trees in the plots ranged from 325 to 1,203 and from 170 to 1,231 trees ha⁻¹ in the first and second surveys, respectively, pointing to an increasing variability and heterogeneity of stand dynamics (Supplementary 2). The strongest decrease in density (irrespectively of recruitment) was observed for *F. excelsior* (by 32.3 trees ha⁻¹), *U. laevis* (18.4 trees ha⁻¹), *Picea abies* (L.) Karst. (11.0 trees ha⁻¹), and *Tilia cordata* Mill. (8.5 trees ha⁻¹) (Table 1). Mostly it was associated with the mortality due to DED and the dieback of *F. excelsior*. Among the common species, the highest tree mortality rates were estimated for *F. excelsior*, *U. glabra*, *P. abies*, and *U. laevis* with the overall mortality of 9.4, 4.5, 4.1, and 1.1% trees (6.5, 7.1, 2.6, and 2.6 trees ha⁻¹) dying annually, respectively. However, the overall mortality largely differed among the stand, with the majority of them (11 of the 18 monitored) showing low values (< 2% of trees year⁻¹), while explicitly high mortality (> 10% of trees year⁻¹) occurred in four (ca. 22%) stands.

Despite the mortality of canopy trees, the total density of the stand between the surveys slowly increased from 606 ± 50.3 to 664.9 ± 55.9 trees ha⁻¹ indicating gradual recruitment of the canopy trees. In 2021, the recruitment of trees of eight species was recorded (Table 2). In one-third of the stands, the canopy self-regenerated explicitly with more than 250 trees ha⁻¹, while in one-fifth of the stands, stagnation without notable recruitment was observed (Supplementary 3). The most common recruiting species were *A. glutinosa* (275.9 ± 92.0 trees ha⁻¹), *Padus avium* Mill. (93.0 ± 40.8 trees ha⁻¹), as well as *U. glabra* (89.6 ± 23.5 trees ha⁻¹) indicating some resilience of the species to the menacing DED. The standing volume of the living canopy trees in the plots between the observations varied considerably ranging between 154 and 700 m³ ha⁻¹. Despite that most trees of large dimensions were dying, only a moderate decrease in standing volume was estimated from 473.1 ± 31.2 to 404.8 ± 32.5 m³ ha⁻¹ in 2016 and 2021, respectively, thus supporting resilience of the stands. Consequently, the deadwood volume in the second observation notably increased (from 132.5 ± 40.8 to 210.2 ± 55.8 m³ ha⁻¹), yet due to the spatially heterogeneous mortality, the quantity of deadwood among the plots also varied greatly locally reaching extreme amounts (from 3.7 to 844.8 m³ ha⁻¹).

The composition of the understory of the plots was richer than that of canopy with 29 tree and shrub species recorded, among which 13 and 16 were AG and UG, respectively (Table 1). Between the surveys, only minor

Species	Acronym	Understory				Canopy			
		2016	2016	2021	2021	2016	2016	2021	2021
		D	O	D	O	D	O	D	O
<i>Alnus glutinosa</i>	<i>AlnuGlut</i>	856	11	789	22	130	33	215	33
<i>Alnus incana</i>	<i>AlnuInca</i>	283	22	14	6		6	16	39
<i>Acer platanoides</i>	<i>AcerPlat</i>	191.63	61	123	78	41	44	60	44
<i>Betula pendula</i>	<i>BetuPend</i>					24	61	18	61
<i>Corylus avellana</i>	<i>CoryAvel</i>	658	44	840	56				
<i>Euonymus europaeus</i>	<i>EuonEuro</i>	90	50	60	44				
<i>Frangula alnus</i>	<i>FranAlnu</i>	14	6						
<i>Fraxinus excelsior</i>	<i>FraxExce</i>	436	72	841	61	71	78	38	78
<i>Grossularia reclinata</i>	<i>GrosRecl</i>	382	6	1910	6				
<i>Lonicera xylosteum</i>	<i>LoniXylo</i>	207	50	495	56				
<i>Malus sylvestris</i>	<i>MaluSylv</i>	42	6						
<i>Picea abies</i>	<i>PiceAbie</i>	53	22	46	22	101	50	90	50
<i>Padus avium</i>	<i>PaduAviu</i>	2416	100	3946	100	60	50	102	61
<i>Populus tremula</i>	<i>PopuTrem</i>			28	6	14	6	14	6
<i>Quercus robur</i>	<i>QuerRobu</i>	19	33	40	33	21	11	21	11
<i>Ribes alpinum</i>	<i>RibeAlpi</i>	42	6						
<i>Rhamnus cathartica</i>	<i>RhamCath</i>	28	11	14	6				
<i>Ribes nigrum</i>	<i>RibeNigr</i>	659	39	766	33				
<i>Ribes rubrum</i>	<i>RibeRubr</i>	42	6	566	6				
<i>Ribes spicatum</i>	<i>RibeSpic</i>	358	17	481	22				
<i>Sorbus aucuparia</i>	<i>SorbAucu</i>	83	39	101	39	35	11	35	11
<i>Salix caprea</i>	<i>SaliCapr</i>			14	6				
<i>Salix cinerea</i>	<i>SaliCine</i>			85	6				
<i>Sambucus nigra</i>	<i>SambNigr</i>	14	6	141	11				
<i>Sorbaria sorbifolia</i>	<i>SorbSorb</i>	71	6						
<i>Tilia cordata</i>	<i>TiliCord</i>	180	22	119	28	93	28	85	33
<i>Ulmus glabra</i>	<i>UlmuGlab</i>	765	67	657	39	173	72	176	72
<i>Ulmus laevis</i>	<i>UlmuLaev</i>	50	44	232	44	400	56	382	56
<i>Viburnum opulus</i>	<i>VibuOpul</i>	141	33	170	11				

Table 1. Understory and canopy species density (D, individuals per ha) and occurrence (O, % of plots present) in the studied *Ulmus* sp. stands

	Density, trees ha ⁻¹	Occurrence, % of plots	DBH, cm	H, m	Standing stock, m ³ ha ⁻¹
<i>Alnus glutinosa</i>	275.87 ± 91.96	11	6.26	6.99	3.65 ± 1.67
<i>Acer platanoides</i>	77.81 ± 21.22	11	6.76	7.26	0.68 ± 0.31
<i>Fraxinus excelsior</i>	14.15	6	5.00	8.50	0.14
<i>Picea abies</i>	84.88	6	7.40	6.93	1.82
<i>Padus avium</i>	92.97 ± 40.82	39	5.73	6.67	0.84 ± 0.36
<i>Sorbus aucuparia</i>	28.29	6	9.35	8.55	0.92
<i>Tilia cordata</i>	33.01 ± 9.43	17	8.23	9.17	0.87 ± 0.23
<i>Ulmus glabra</i>	89.60 ± 23.45	67	6.83	8.76	1.67 ± 0.39
<i>Ulmus laevis</i>	28.29	6	7.40	6.00	0.45

Table 2. Tree density, occurrence and dimensions of new accounted canopy trees in *Ulmus* sp. stands

changes in the composition occurred, as a single AG species (common aspen *Populus tremula* L.) and two UG species appeared, while three UG species disappeared. The occurrence (presence in stands) of *Acer platanoides* L. and *A. glutinosa* in AG increased, while that of *U. glabra* and *F. excelsior* decreased. Regarding UG, the occurrence shifted for several species, but notable changes were observed only for *Corylus avellana* L. (increase) and *Viburnum opulus* L. (decrease) (Table 1). Accordingly, the composition of undergrowth was generally stable, with the changes being local rather than regionally systematic, as supported by low and significant dissimilarity between the observations ($R = 0.002$; $p = 0.04$), as revealed by the ANOSIM.

Substantial changes were estimated for the abundance of understory, which increased in 82% of the plots. The increase in understory density ranged from 56 to 1430%, particularly due to rapid recruitment of UG, which nearly doubled from $3,282.9 \pm 614.4$ in 2016 compared with $5,293.4 \pm 813.3$ individuals ha⁻¹ in 2021 (Figure 2). The density of AG remained stable ranging from $1,180.5 \pm 220.6$ to $1,208.0 \pm 343.7$ individuals ha⁻¹ in 2016 and 2021, respectively. Hence, the ratios of AG and UG individuals shifted from 26 and 74% to 19 and 81% in 2016 and 2021, respectively, indicating that AG was suffering increasing competition.

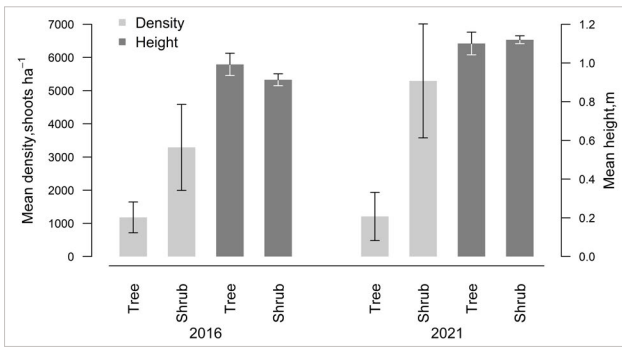


Figure 2. Mean density and height (\pm SE) of advance growth and undergrowth/shrubs on the permanent sampling plots in the mature stands of *Ulmus* sp. in Latvia

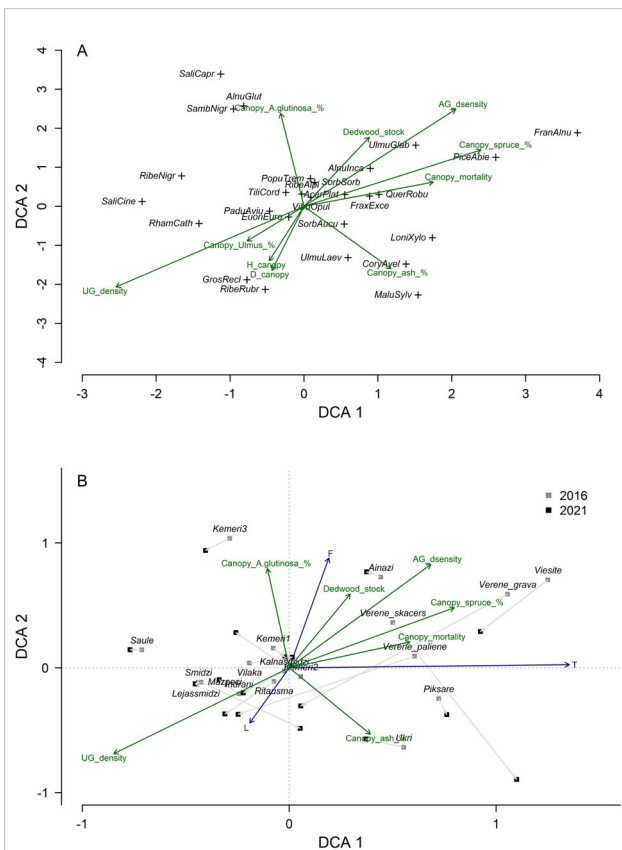


Figure 3. The DCA ordination of understory (advanced growth and undergrowth) species (A) and sample plots (B) according to their relative abundance (density) in *Ulmus* sp. stands in Latvia in 2016 and 2021

The successional changes in species composition among the observations are indicated by the grey vectors (B). For species acronyms, see in Table 1. The green (centered) vectors indicate correlations of the gradients with stand and site properties. Abbreviations of the vector names: T – temperature, F – moisture, L – light, D_canopy – canopy diameter, H_canopy – canopy height, Dedwood_stock – dedwood stock, Canopy_Ulmus_% – proportion of elms in canopy, Canopy_spruce_% – proportion of *P. abies* in canopy, Canopy_ash_% – proportion of *F. excelsior* in canopy, Canopy_A.glutinosa_% – proportion of *A. glutinosa* in canopy, AG_density – AG density, UG_density – UG density, Canopy_mortality – canopy mortality.

During both study periods, AG of *A. glutinosa* (811 trees ha⁻¹), *U. glabra* (725 trees ha⁻¹), and *F. excelsior* (621 trees ha⁻¹) had the highest density. In 2021, a significant increase in density was observed for the declining *F. excelsior* and *U. laevis*, indicating their resilience and self-regeneration, although the density of *U. glabra* plummeted (Table 1). In UG, the density of *P. avium* (3,181 individuals ha⁻¹), *C. avellana* (759 individuals ha⁻¹), and *Ribes nigrum* L. (708 individuals ha⁻¹) have remained constantly high, while an increase occurred mainly for the garden-refugees, e.g. *Grossularia reclinata* (L.) Mill. and *Ribes* sp. (Table 1). Despite the rapid increase in the number of UG recruits, the mean height of AG and UG remained similar ($p = 0.21$) and slowly increased with time (Figure 2).

Across the studied network of PSP, two continuous principal gradients of understory trees and shrubs were estimated by the DCA, indicating systematic environmental effects on the regeneration of the stands (Figure 3A, B). The main gradient represented by the first axis of DCA was related to Ellenberg’s indicator values of temperature and light, and the proportion of Norway spruce in the canopy (Figure 3A, B; Table 3), which were not collinear. The effects of these stand properties were also supported by the species ordinations (Figure 3A). The adventitious and/or temporary species (e.g. *G. reclinata* and *Ribes rubrum* L.) were related to the high light part of the gradient. However, the high temperature part of the gradient was associated with a narrow set of undergrowth species (except *Frangula alnus* Mill.), and hence with lower species richness in UG (correlation). In contrast, most saplings (AG; *U. laevis*, *T. cordata*, *P. tremula*, *A. platanoides*, *F. excelsior*, and *Alnus incana* (L.) Moench.) were associated with medium or low temperature and medium light conditions. Only AG of *U. glabra* and *A. glutinosa* was associated with medi-

Table 3. The relationships between the first two gradients of ground cover vegetation in the studied elm stands and stand properties

	χ^2	p-value
DCA1		
<i>Fixed effects</i>		
Temperature	75.6	< 0.001
Light	5.4	0.02
Spruce in canopy, %	5.5	0.02
<i>Model performance</i>		
R ² , marginal		0.75
R ² , conditional		0.92
DCA2		
<i>Fixed effects</i>		
Moisture	18.3	< 0.001
AG density	9.3	0.002
Black alder in canopy, %	7.1	0.008
Ash in canopy, %	4.8	0.003
<i>Model performance</i>		
R ² , marginal		0.62
R ² , conditional		0.63

um temperature and shade conditions. The second gradient was correlated with Ellenberg's indicator value moisture (F), the proportion of black alder and ash in the canopy, as well as AG density (Table 3), particularly that of *A. glutinosa* and *U. glabra* (Figure 3A). Hence, the two principal gradients indicated that regeneration and succession after partial canopy mortality was affected by altered microclimate. Accordingly, the recruiting AG preferred moist, medium light and temperature conditions, while UG was more flexible and hence competitive.

The ordination of plots showed that half of the stands were highly similar in terms of understory (AG and UG), as well as successional changes in it. Nevertheless, the others showed a wide range of scores of the first two gradients indicating the diversity of site conditions, as well as highly varying successional changes (Figure 3B). The range of the DCA scores of the plots appeared related to the dominant canopy species, hence the stands dominated by elms (and denser UG) mainly showed the highest similarity and the smallest (low to moderate) successional changes in the understory. The successional changes were mostly related to the shift in the ratio of AG and UG abundances, which was affected by both estimated gradients, indicating complex effects of light, temperature, moisture, and the share of conifers in the canopy. Still, most of the stands tended to increase the share of UG in the understory (leftwards pointing arrows) leaning to more light-dependent and less thermophilic communities, with only a few stands showing the opposite. Regarding the moisture gradients (according to Ellenberg's value), changes in understory composition shifted towards the communities favouring lower moisture drier conditions, indicating the effects of water shortage. Nevertheless, the short successional vectors indicated that some plots (e.g. in Saule, Kemerī 1, Indrani, and Ainazi) were stable in the composition and abundance of AG and UG. These stands, though, might also be characterized by low mortality or very recent changes in the canopy, to which the understory has not responded yet. Accordingly, the estimated changes in the understory of the studied stands indicated an ongoing shift in succession, including the establishment of a shrubland phase. However, the positive correlation between AG density and canopy tree mortality suggests some self-regeneration.

Discussion

The DED in Europe has been confirmed since the beginning of the 20th century (Brasier 1990), yet Northern Europe has likely been relatively shielded from the infestation by cooler/harsher climate (La Porta et al. 2008). The anticipated climate change, hence, appears alarming regarding the surges in DED in the northern part of elms distribution (Solheim et al. 2010). Nevertheless, the estimated mortality of elms in Latvia was lower (Table 1) compared to Eastern Europe (Czeszczewik et al. 2022), while being comparable to other Nordic countries (Solheim et al. 2011,

Jürisoo et al. 2019, Ruks 2020), suggesting some resilience of eastern Baltic populations. Furthermore, the increase in the stand (canopy tree) density highlighted self-regeneration, as the conditions favour deciduous species (Kellomäki et al. 2018). Most of the stands still suffered low mortality of canopy trees indicating resistance of mixed forests, even though compositional richness (4–7 species) was intermediate for broadleaved hemiboreal stands (Jactel et al. 2017). Besides elms, an explicit decrease was observed in the abundance of *F. excelsior* and *P. abies*, suggesting complex effects of climatic changes (Seidl et al. 2017).

In Latvia, DED has been reported relatively late (Matisone et al. 2020), presuming some resistance to the latitudinal spread of the pathogens. However, elms in Latvia have probably already experienced the first wave of DED, as 18% (~ 61 trees ha⁻¹) of elms were dead at the beginning of the observations in 2016 (Table 1). The excessive elm mortality occurred in the few stands previously co-dominated by *F. excelsior*, which has suffered excessive dieback before (Pušpure et al. 2016, Matisone et al. 2018), indicating legacy effects of an intensive disturbance (Seidl et al. 2017). The mortality rate of *U. laevis* was minimal (1.1% year⁻¹; Table 1), similar to that in neighbouring Estonia, where no dead trees were reported until 2019 (Jürisoo et al. 2019). Such lower mortality might be explained by the disease vectors, particularly *Scolytus* sp., which prefer *U. glabra* over *U. laevis* (Webber 2000, Collin 2003). Nevertheless, the estimated mortality rates highlighted spatially heterogeneous susceptibility of elms (Guries and Smalley 2000). The dating of the estimated mortality across the region also suggests that the virulence of the disease might have decreased over time (Berngruber et al. 2013), as supported by the recent stabilization/recovery of elm populations in Poland, where DED has been present for several decades (Czeszczewik et al. 2022).

As the studied stands suffered different degree of dieback of canopy trees resulting in canopy opening, light was estimated as the main environmental driver of the understory (Table 3). Complementary to light availability, canopy openings affect microclimate (Brunet et al. 2023), particularly the moisture regime in the studied stands, which was estimated as the second principal gradient (Table 3). The mortality of canopy elms and the state of AG differed among the stands (Figures 2, 3; Supplementary 2), thus indicating the effects of local/stand conditions along the identified gradients, particularly considering the occurrence near the periphery of the elms' range (Solheim et al. 2011, Jürisoo et al. 2019, Czeszczewik et al. 2022). Such local effects have been diverging successional changes of elms stands (Figure 3B), leading to disproportional changes in broadleaved forests (Hytteborn et al. 2017, Czeszczewik et al. 2022).

In half of the stands, the understory has undergone explicit compositional changes, particularly as the stand microclimate has been altered (Brunet et al. 2023). The AG preferred specific (moist, medium light and temperature) environmental conditions (Figure 3B, Table 3), which are

characteristic in stands after partial canopy dieback (Brunet et al. 2014), while the UG species rapidly occupy dieback-induced canopy gaps (Ehrenfeld 1980, Huenneke 1983). The abundance of AG, however, was related to the mid-part of the gradient, implying that moderate conditions are needed for successful regeneration of canopy species (Pušpure et al. 2016). The explicit advance of UG, in turn, appeared related to their plasticity regarding light conditions and moisture (Huenneke 1983, Brunet et al. 2023), as highlighted by the ordination (Figure 3).

Previously, gaps in elm stands created by DED and other disturbances have been recolonized by ash, but currently both species are being restricted to understory with low to moderate cover (Peterken and Mountford 1998, Brunet et al. 2014, Brunet et al. 2023). Accordingly, *P. avium* and *C. avellana*, and neighbouring canopy species rapidly colonized openings (Supplementary 2) facilitating the formation of semi-stable shrubland phase (Huenneke 1983, Hytteborn et al. 2017, Nestby 2020). Furthermore, the more open canopy conditions might increase the effects of drought (Allen et al. 2015) and competitiveness of the herb layer over elm AG (Jochner-Oette et al. 2021). The increase of adventitious and/or temporary UG species (e.g. *G. reclinata* and *Ribes* sp.) (Table 1), particularly in response to increased light availability (Figure 3), also implied that DED caused relatively intensive disturbances, opening a gateway for invasion (Terwei et al. 2013). Furthermore, in 17% of the stands, no recruiting canopy trees were accounted suggesting a possibility of a gradual decline (Supplementary 3), although the underlying causes (seed sources, UG density, light availability, etc.) were diverse and likely complex. It might thus be speculated that a long time (100–200 years) might be needed for the natural recovery to occur (Shugart and West 1977, McCormick and Platt 1980). In some cases, though, the development of AG and recruitment may be delayed (Oldfield and Peterson 2019).

Irrespective of geographic location, half of the stands remained relatively stable in terms of canopy and understory and showed AG and canopy recruitment of elms (Table 1, Figure 3, Supplementary 2, 3), cherishing some hopes for the continuity of elm admixed stands (Jürisoo et al. 2019, Brunet et al. 2023). The comparable height of AG and UG suggested balanced competition (Pušpure et al. 2016, Hytteborn et al. 2017, Gleason et al. 2018), likely as AG appeared able to benefit from the surplus light provided by the canopy (shelterwood) opening (Figure 3). Such balance, though, might be shifted by browsing (Suleková and Kodrik 2011), which however was negligible in the PSPs. Still, despite the stability of composition and density of AG, UG density was increasing (Figure 2), rising competition to the recruiting canopy trees (Gleason et al. 2018, Oldfield and Peterson 2019), thus drawing parallels with the effects of *F. excelsior* dieback (Pušpure et al. 2016). The share of conifers in the canopy was significant for AG (Figure 3, Table 3), likely due to effects on soil reac-

tion (Augusto et al. 2015) and root contacts, which affect sampling vigour and spread of DED (Santini and Faccoli 2015). This suggests the stability of conifer-broadleaved mixtures (Jactel et al. 2017), which are naturally occurring in the hemiboreal zone (Saarse and Veski 2001, Forest Europe 2015). Nevertheless, under the diverging successional changes (Figure 3), it is difficult to project the general development of the affected elm stands, as the surviving trees tend to decrease growth (Peterken and Mountford 1998), and the recruiting trees tend to be infected once DBH exceeds 10 cm (Brunet et al. 2014), as well as reinfection might occur (Harwood et al. 2011, Łakomy et al. 2016). Also, a high density of saplings/recruiting trees might have a negative impact due to density-dependent pest-host interactions (Flower et al. 2017), and more frequent root contacts (Santini and Faccoli 2015).

The advances of DED as a large-scale biological invasion had diverging effects on elm forests in Latvia diversifying the development of the affected stands. Though in contrast to Sweden, where all native elm species (*U. glabra*, *U. laevis*, *U. minor*) are critically endangered (Barstow and Harvey-Brown 2017, Barstow and Rivers 2017), in Eastern Europe (cf. Czeszczewik et al. 2022) and in the Baltics, the abundance of elms has decreased moderately, signifying unlikely extinction of elms. Due to elm-specific habitat, they often occur in protected areas in Europe (Litkowiec et al. 2022) including Latvia (Laiviņš et al. 2009), hence specific protection is not imminent, yet monitoring of health condition is advisable (Collin 2003, Venturas et al. 2014). Still, due to the additional disturbance caused by DED in broadleaved stands in Latvia, a partial decrease in canopy richness might be expected (Hytteborn et al. 2017).

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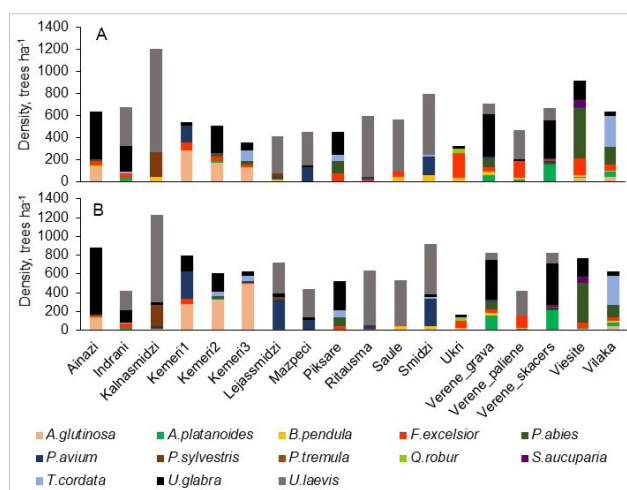
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Supplements

Supplementary 1. Characteristics of the studied *Ulmus* sp. stands

Site	Area, ha	Age, years	Moisture regime	Fertility	Soil type
Ainazi	1.60	120	dry	eutrophic	drained peat
Indrani	3.19	68	dry	mesotrophic	mineral
Kalnasmidzi	1.27	75	dry	mesotrophic	mineral
Kemer1	6.43	108	periodically waterlogged	eutrophic	shallow peat
Kemer2	3.70	128	periodically waterlogged	eutrophic	shallow peat
Kemer3	3.70	128	periodically waterlogged	eutrophic	shallow peat
Lejassmidzi	1.27	75	dry	mesotrophic	mineral
Mazpeci	0.96	89	dry	mesotrophic	mineral
Piksare	2.67	140	dry	mesotrophic	mineral
Ritausma	0.45	104	dry	eutrophic	mineral
Saule	0.51	69	dry	mesotrophic	mineral
Smidzi	3.86	56	dry	mesotrophic	drained mineral
Ukri	1.04	111	dry	mesotrophic	mineral
Verene_grava	6.34	143	periodically waterlogged	mesotrophic	mineral
Verene_paliene	6.34	143	periodically waterlogged	mesotrophic	mineral
Verene_skacers	6.34	143	periodically waterlogged	mesotrophic	mineral
Viesite	0.97	121	dry	mesotrophic	mineral
Vilaka	0.67	78	dry	mesotrophic	drained peat

Supplementary 2. Canopy species density and composition of the studied *Ulmus* sp. stands in 2016 (A) and 2021 (B)



Supplementary 3. Density and composition of new accounted canopy species in the studied *Ulmus* sp. stands

