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Soil pH and Organic Matter Content Affects European Ash (*Fraxinus excelsior* L.) Crown Defoliation and Its Impact on Understory Vegetation

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Abstract: European ash (*Fraxinus excelsior* L.) dieback caused by the fungus *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz, and Hosoya has been affecting European forests since 1992. The disease drives severe crown defoliation, branch loss, and finally tree mortality in European ash. The environmental factors affecting the disease process are still not fully recognized. We hypothesized that the level of crown defoliation in ash, as well as its impact on understory vegetation, will differ along the pH gradient in soil. We examined 27 ash stands in western Poland. We assessed the crown defoliation of 15 dominant and co-dominant trees, soil parameters (pH and soil organic matter contents; SOM), and also recorded the understory vegetation species composition. Most moderately and severely damaged trees occurred within the plots with a high SOM content (>7.5%) and neutral to slightly alkaline soil pH (>7.0) in the A horizon. We noted significantly lower crown defoliation in mesic sites with acidic soils and lower SOM contents. The results also showed the influence of ash crown defoliation on the species functional composition. Ash dieback led to the creation of gaps, and their colonization by other species frequently found in forest sites, especially forest-edge tall herbs.

Keywords: ash dieback; functional diversity; *Hymenoscyphus fraxineus*; soil organic matter; broadleaved forest; tree mortality

1. Introduction

Global changes in the environment induce novel phenomena that change the distributions of tree species [1,2]. The *Fraxinus* genus is one of the most visible examples of retreat. In North America, the trees are threatened by the Emerald ash borer (*Agrilus planipennis* Fairmaire) which primarily infest and can cause significant damage to ash species, including *Fraxinus pennsylvanica* Marsh., *F. nigra* Marsh., *F. americana* L., and *F. quadrangulata* Michx. [3]. This beetle has also been noted in Europe and is suggested as the main potential pest of European ash (*F. excelsior* L.) [4]. Moreover, ash is threatened by climate change; the increase in average temperatures during the growing season and reduced atmospheric precipitation especially cause the disappearance of ash from its typical sites [5]. Another factor threatening ash is the fungal disease caused by the ascomycete *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz and Hosoya [6]. The disease causes ash loss or severe crown defoliation. Consequently, it can cause an ecological cascade effect in ash sites, resulting in the retreat of dependent organisms, e.g., invertebrates, epiphytic bryophytes, and lichens [7], as well as understory vegetation [8]. Changes in the understory are thought to be driven initially by increased light because of the opening up of the canopy as the ash overstory disappears, followed by increases in the shrub layer or canopy closure by other tree species [9].

The first symptoms of ash dieback were observed in 1992 in NE Poland [10]. Within a few years, the disease had spread to all Polish populations of ash, causing the dieback of nearly 10,800 ha of ash stands [11]. In 1995–1996, similar symptoms appeared in Lithuania. This led to a decrease in the area of ash stands from 50,800 ha in 1995 to 36,300 ha in 2011 [12,13]. By 2016, the disease had spread to more than 25 European countries, with up to 85% and 69% mortality rates recorded in plantations and woodlands, respectively [14–16]. The fungus infection starts during the summer when the ascospores land on the leaves. The ascospores germinate on the rachis and petioles [17,18]. In the further stadium, the fungal spores infect stems and branches, causing local necrosis [19]. These necrotic lesions then enlarge and stretch causing perennial cankers on branches, leaves shedding and wilting, and finally death of the top of the crown [20–22].

The origin of the pathogen in Europe has been associated with its introduction from *F. mandshurica* Rupr. and *F. chinensis* Roxb. [23–25]. The highest rates of damage were recorded on *F. excelsior* and *F. angustifolia* Vahl. Significantly lower damage rates were found on other ash species introduced to Europe [26]. Additionally, in vitro studies have shown that the fungus develops best in moist conditions, in a temperature range of 15–25 °C [27].

Studies across Europe associate ash dieback with moist and fertile soils, as well as the dominance of ash in forest [22]. For instance, in Austria, the Czech Republic, Slovakia, and Ukraine, the highest mortality rates were reported in moist and floodplain forests [13,28–30]. In Latvia, ash dieback and its natural regeneration varies significantly depending on the soil conditions. The lowest decline was observed in dry and mineral soils [31,32]. This is in accordance with a few studies stating that trees are more infected in optimal ash sites, characterized by calcareous (pH values above 5–6) and organic soils with shallow groundwater [33–35]. In contrast, ash can also grow in suboptimal growth conditions, on mesic sites, with more acidic mineral soils with lower groundwater levels [36]. In such conditions, ash trees revealed less symptoms of disease [11]. Other studies have shown that the development of the fungus and the intensity of symptoms also decreased in dry conditions, except in extremely dry and low-temperature sites [37].

The literature shows that *H. fraxineus* spread is still ongoing, and the large scale of its occurrence in different site conditions makes it difficult to assess the importance of environmental parameters on its performance. It also suggests that soil parameters might be an important factor influencing the impact of fungus on ash stands. Considering this, we are aware that the referenced studies usually used abstract units, such as soil types and forest site categories, rather than strict measurements of soil characteristics. That is why in our study we present strict values of chosen soil factors that may have an effect on ash crown defoliation. This brings a new perspective to the ash dieback process and expands the results of Erfmeier et al. [38], who investigated the impact of forest types on the condition of ash. The authors studied a wide habitat gradient, and the forest type could outweigh the actual soil parameters. In our study, we have chosen a more continuous gradient of forest types in which ash is found; hence, we expect to see the impact of soil factors that have a biological effect on ash dieback.

In this study, we assessed whether the ash condition may depend on soil parameters. We hypothesized that (1) tree crown defoliation will be lower in more acidic soils and (2) in soils with lower organic matter contents, similar to broad-scale studies based on forest types [11,28–31,37,38]. Moreover, we also hypothesized (3) that crown defoliation will affect understory species change and functional composition, by increasing the proportion of competitive forest-edge tall herbs.

2. Materials and Methods

2.1. Study Area

The study was conducted in July and August 2016 in the Babki, Konstantynowo, and Łopuchówko forest districts in the Wielkopolska Region (western Poland). The average annual rainfall recorded at the meteorological station at Zielonka (17°6′25″ E, 52°33′18″ N) was 525 mm for the years 1986–2008. Although the trend line for precipitation is relatively constant, the annual sum of rainfall differed significantly in individual years (from 312 mm in 1989 to 724 mm in 1993). The average annual air temperature was 8.3 °C [39]. The vegetation period lasts 220–230 days [40]. The landscape is shaped mostly by glacial and postglacial formations affecting the soil properties and plant species composition [41]. Within our study plots, we described a few groups of soils: Phaeozems, Umbrisols, Luvisols, Gleyosols, Cambisols, and Arenosols (Table 1). Such environmental conditions affect the proportion of ash in the stand species composition. In the studied area, ash is an important forest-forming component of mixed stands along the river valleys and lakesides (Figure 1). It grows in riparian forests as the dominant and co-dominant species. Its occurrence within such sites is associated in various proportions with *Alnus glutinosa* Gaertn., *Ulmus laevis* Pall., *U. glabra* Huds., or *Quercus robur* L. As an admixture, it grows additionally within moist and mesic broadleaved forests, with a higher proportion of *Q. robur* and *Tilia cordata* Mill. (Table 1). The study was carried out in 27 plots. The age of ash stands, according to forest management plans, ranged from 48 to 144 years (Table 1; Figure 1).

Table 1. Basic characteristics of the study plots. Reference soil groups and their principal and supplementary qualifiers follow the IUSS Working Group WRB [42]. Forest districts: B (Babki); K (Konstantynowo); L (Łopuchówko); P (Poznań Communal Forests). Species abbreviations: A (*A. glutinosa*); F (*F. excelsior*); T (*T. cordata*); U (*U. laevis*, *U. glabra*); Q (*Q. robur*). Coordinates follow the World Geodetic System '84.

No.	District Division	Main Tree Species Proportion (%)	Ash Age	Soil Characteristic WRB 2015	Coordinates of the Study Plots N	E
1.	B 243c	90 F, 10 Q	79	Arenic Gleyic Phaeozem	52°26'37.692"	17°4'6.244"
2.	B 231l	90 F, 10 U	57	Colluvic Greyzernic Phaeozem	52°27'6.107"	17°4'41.754"
3.	B 225d	80 F, 10 Q, 10 T	100	Ochric Brunic Arenosol	52°27'30.791"	17°4'19.11"
4.	B 218b	100 F	114	Colluvic Gleyic Phaeozem	52°27'29.987"	17°4'3.955"
5.	B 226d	80 F, 10 L, 10 Q	87	Colluvic Fluvic Cambisol	52°26'58.596"	17°3'39.512"
6.	B 224i	80 F, 10 U, 10 Q	102	Siltic Gleyic Phaeozem	52°27'31.461"	17°4'26.068"
7.	B 224h	80 F, 10 U, 10 Q	120	Colluvic Fluvic Cambisol	52°27'33.842"	17°4'24.141"
8.	B 224c	80 F, 20 Q	52	Arenic Calcaric Cambisol	52°27'40.327"	17°4'46.34"
9.	B 223i	90 F, 10 Q	85	Arenic Calcaric Cambisol	52°27'44.637"	17°4'48.887"
10.	K 281c	90 F, 10 U	106	Hyperhumic Gleyic Phaeozem	52°13'11.121"	16°43'39.585"
11.	K 282b	80 F, 20 A	73	Hyperhumic Gleyic Phaeozem	52°13'24.06"	16°43'25.671"
12.	K 286a	90 F, 10 U	109	Humic Mollic Gleysol	52°13'9.247"	16°44'25.939"
13.	K 287d	100 F	52	Humic Mollic Gleysol	52°13'8.269"	16°44'14.987"
14.	K 287h	90 F, 10 Q	123	Ochric Brunic Arenosol	52°13'4.573"	16°44'6.423"
15.	K 288a	90 F, 10 U	119	Hyperhumic Gleyic Phaeozem	52°13'4.05"	16°44'3.199"
16.	K 288j	90 F, 10 U	79	Hyperhumic Gleyic Phaeozem	52°13'0.473"	16°44'0.881"
17.	K 59b	80 F, 20 Q	68	Ochric Brunic Arenosol	52°12'52.495"	16°44'1.288"
18.	L 257a	90 F, 10 Q	144	Loamic Dystric Cambisol	52°29'49.713"	16°57'3.233"
19.	L 255s	100 F	98	Arenic Fluvic Cambisol	52°29'30.49"	16°57'53.237"
20.	L 254h	80 F, 20 A	74	Humic Gleyic Fluvisol	52°29'46.855"	16°57'53.582"
21.	L 251c	80 F, 10 U, 10 A	69	Humic Gleyic Fluvisol	52°30'17.183"	16°57'44.836"
22.	L 217g	90 F, 10 A	68	Humic Gleyic Fluvisol	52°30'23.024"	16°57'6.738"
23.	L 205d	80 F, 20 Q	74	Colluvic Fluvic Cambisol	52°30'41.062"	16°56'34.311"
24.	P 475j (1)	100 F	83	Siltic Gleyic Phaeozem	52°25'23.309"	16°52'58.823"
25.	P 475j (2)	90 F, 10 U	83	Siltic Gleyic Phaeozem	52°25'27.169"	16°52'36.643"
26.	P 473d	80 F, 10 T, 10 Q	63	Hyperhumic Gleyic Phaeozem	52°26'1.955"	16°52'39.371"
27.	P 430k	100 F	73	Clayic Haplic Luvisol	52°24'16.2"	17°1'30.72"

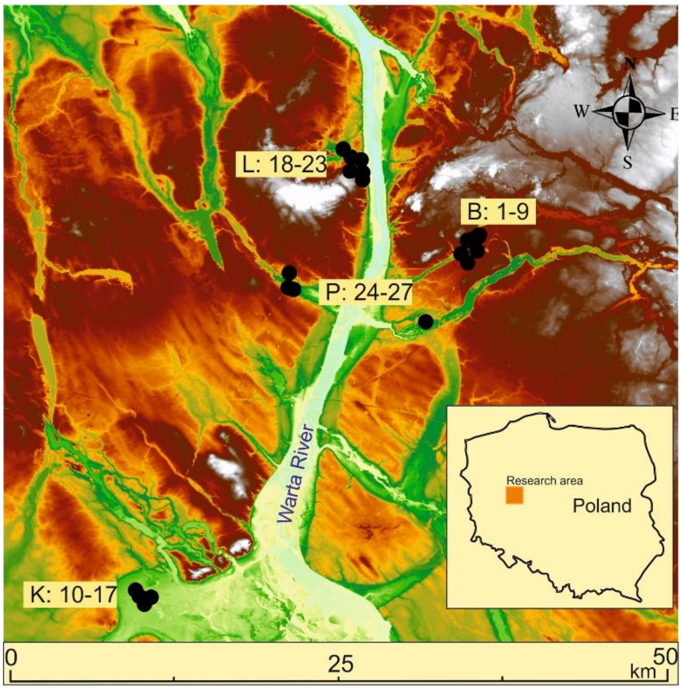

Figure 1. Location of the study plots in the background of the hypsometric map. The succession of colors reflects the relief from the highest places (white), through brown, yellow, to the lowest places marked in green (river valleys) and in light blue (rivers). Abbreviations of forest districts: B (Babki); K (Konstantynowo); L (Łopuchówko); P (Poznań Communal Forests). Coordinates of the study plots are placed in the Table 1.

2.2. Study Design

We located the study plots within the part of the stands with at least 80% proportion of ash in the stand species composition. The size of each plot was 2500 m^2. In the central part of each study plot, we chose 15 ash trees. Trees were selected according to the biosocial position, assessed using Kraft's classification [43]. We randomly selected only dominant and co-dominant trees, excluding trees where we could not assess the defoliation.

Because of high level of ash trees infestation by ash dieback in Poland and lack of other potential drivers of defoliation we assumed that ash defoliation in the study area was caused by ash dieback. Although this assumption is not based on detection of disease and compromise only indirect measure of ash dieback, we decided to focus on manifestation of the disease rather than its presence. We assessed the crown defoliation visually with 5% precision [44,45]. Subsequently, we assigned the crown defoliation to the damage classes described by Hanisch and Kilz [46]. As a response variable describing the level of defoliation, we used the mean crown defoliation and proportions of moderately damaged trees (third class of damage, with defoliation between 25–60%) and severely damaged trees (fourth class of damage, with defoliation >60%).

2.3. Soil Characteristics

We assessed the soil characteristics by digging a pit in the middle of each study plot. The depth of the soil pit was 2 m, or in case of moist soils, the depth to the groundwater level. We studied the soil profile and sampled 500 g of soil from each soil horizon. We determined the soil pH measured in distilled water (potentiometric method) in the laboratory. Moreover, we analyzed the percentage content of organic carbon (Tiurin's method), which was recalculated into the percentage content of SOM using the factor 1.724 [47].

2.4. Vegetation Characteristics

Within each plot, we noted covers of all vascular plants and bryophytes species using the Braun-Blanquet scale. The survey was conducted on an area of 400 m^2 in the middle of each study plot. The cover of plant species was assessed separately for each forest strata in April and July, and then pooled, to account for all species occurring in the understory by the year. These two dates are representative for floodplain forests, as Czapiewska et al. [48] revealed that April and July are close to the centroid points representing seasonal shifts in understory vegetation seasonal composition; the above-mentioned study was conducted in our study area. During the study, we tallied only the understory layer, as shrubs and trees in parts of the forests were artificially planted and thus did not account for the spontaneous process of plant community assembly. In Figure 3, the abbreviations of the names of the following plant species are given: *Adoxmosc*, *Adoxa moschatelina*; *Aegopoda*, *Aegopodium podagraria*; *Allipeti*, *Alliaria petiolata*; *Anemnemo*, *Anemone nemorosa*; *Anemranu*, *A. ranunculoides*; *Arctnemo*, *Arctium nemorosum*; *Asareuro*, *Asarum europaeum*; *Bracsylv*, *Brachypodium sylvaticum*; *Carexacut*, *Carex acutifolia*; *Chaetemu*, *Chaerophyllum temulum*; *Cirsoler*, *Cirsium oleraceum*; *Convmaja*, *Convallaria majalis*; *Dryomas*, *Dryopteris filix-mas*; *Festgiga*, *Festuca gigantea*; *Ficavern*, *Ficaria verna*; *Fraxexce*, *Fraxinus excelsior*; *Galiapar*, *Galium aparine*; *Gerarobe*, *Geranium robertianum*; *Geumurba*, *Geum urbanum*; *Glechhede*, *Glechoma hederacea*; *Humulupu*, *Humulus lupulus*; *Impaparv*, *Impatiens parviflora*; *Maiabifo*, *Majanthemum bifolium*; *Mercpere*, *Mercurialis perennis*; *Mohetrin*, *Moheringia trinervia*; *Oxyrhian*, *Oxyrrhynchium hians*; *Pariquad*, *Paris quadrifolia*; *Plagundu*, *Plagiomnium undulatum*; *Poanemo*, *Poa nemoralis*; *Rubufrut*, *Rubus fruticosus*; *Rubuidae*, *R. idaeus*; *Stacsylv*, *Stachys sylvatica*; *Stelmedia*, *Stellaria media*; and *Urtidioi*, *Urtica dioica*.

We used ecological indicator values (EIVs) of light, moisture, soil reaction, and fertility, provided by Ellenberg and Leuschner [49], to describe the understory vegetation. EIVs describe species ecological requirements, which may reflect their reaction to an increased or decreased availability of resources. We also described the understory vegetation in terms of its species functional traits: height, leaf mass, size, dry matter content, specific leaf area (SLA), growth form, seed mass, and seed number per shoot and life strategy. These data were obtained from the LEDA database, covering the values of these traits for each species [50]. All of the traits and EIVs were used to calculate two components of functional diversity: functional evenness (FEve) and functional dispersion (FDis). FEve describes the regularity of spacing between species in the trait space, while FDis describes the range of species dispersion within trait hypervolumes [51–53]. We calculated FEve and FDis using the *FD::dbFD*() function [54]. We used the community-weighted mean (CWM) values of height, seed mass, and SLA to assess potential shifts in community functional composition along with gradients of defoliation or soil pH. We chose these three traits as they most clearly describe the economical spectrum and life strategies of plants [55–57]. We also calculated the indices of taxonomic diversity: the species richness and Shannon diversity indices.

2.5. Data Analysis

All analyses were conducted using R software (The R Foundation for Statistical Computing Platform; Vienna, Austria, version 3.5.3) [58]. We assessed the impact of soil pH and SOM content on defoliation using generalized linear models assuming the beta distribution of the dependent variable and logit link function, implemented in the *betareg::betareg*() function [59]. In the case that there were fractions of severely defoliated species, which were absent in five of 27 study plots, we used a zero-inflated model, implemented in the *gamlss::gamlss*() function [60]. We decided to use models assuming beta distribution, as this better reflects the proportional data (fraction of trees meeting the given condition) than Gaussian distribution. We started with models containing all three predictors and using Akaike information criterion with small-sample correction (AICc) we choose the most parsimonious model. AICc is a metric showing ratio of variance explained by the model to number of independent variables. For that reason including additional variables not increasing amount of explained variance (predictive power) of the model is penalized, as log-likehood of the model is divided by the number of predictors. To assess its fitness, we reported the AICc of the final model, AICc of the null model (intercept-only; $AICc_0$), log-likelihood, and pseudo-coefficient of determination as an estimation of the proportion of explained variance [61]. Before analyses, we ensured that there were no high intercorrelations between variables using variance inflation factors (all < 2). In the models we did not account for the stand age, as we did not find a significant impact of age on the mean defoliation (effect size = 0.0027 ± 0.0053 per year, according to the beta regression model), nor on the proportions of moderately and severely damaged trees and severely damaged trees (0.0064 ± 0.0064 and −0.0002 ± 0.0094, respectively). We did not include spatial autocorrelation in the models as close neighboring study plots differed in terms of soil or stand parameters (Table 1), which are major drivers of ash growth [5,35,36].

We assessed the impact of soil variables and defoliation on species composition using redundancy analysis (RDA), implemented in the *vegan::rda*() function [62]. RDA is the extension of principal component analysis, where the results (site and species scores) are constrained by environmental variables. We chose RDA instead of other ordination methods because of the short and linear gradient of species composition, revealed by preliminary unconstrained ordinations. Prior to analyses, we transformed species cover using Hellinger's square-root transformation, implemented in the *vegan::decostand*() function [62]. We selected constraining environmental variables using Akaike information criterion (AIC) (as AICc is not available in the vegan package) and we tested their goodness of fit using permutation analysis of variance (PERMANOVA) implemented in the *vegan::anova.cca*() function [62]. To assess whether vegetation characteristics differ along species composition gradients we projected them passively (i.e., without influencing the site and species scores) onto the RDA result using the *vegan::envfit*() function [62]. We did not use these features as constraints, as all of them are derived from species composition; thus, their usage would lead to circular reasoning.

3. Results

Mean crown defoliation, as well as the proportion of moderately and severely damaged trees, were positively correlated with the soil pH and SOM content in the A horizon (Tables 2 and 3; Figure 2). However, in case of defoliation, soil pH had almost half the effect in terms of the proportions of moderately and severely damaged trees. Mean defoliation reached values over 50% in soils with pH values above 7.0. However, in the model explaining proportion of moderately and severely damaged trees, such trend was less clear than that in case of the model explaining mean defoliation. According to AICc of models, the final model explaining the proportion of severely damaged trees only comprised the SOM content (Table 4; Figure 2). Mean defoliation was the most explained model among the studied depended variables, while proportion of severely damaged trees was the least explained.

Table 2. Beta regression model of the mean defoliation of *Fraxinus excelsior* (n = 27).

Term	Estimate	SE	Z	Pr(>|z|)
(Intercept)	−2.627	0.776	−3.384	0.001
Soil pH	0.230	0.127	1.809	0.070
Soil organic matter	0.090	0.031	2.918	0.004
Precision parameter φ	18.955	5.047	3.756	<0.001
Pseudo-R^2	logLik	AICc	$AICc_0$	df of residuals
0.525	23.146	−36.474	−22.403	23

Abbreviations: SE – standard error, Z – empirical test statistic, Pr(>|z|) – p-value, based on comparison of empiric and tabular Z, logLik – log-likelihood, AIC_c – model's Akaike's Information Criterion corrected for small sample size, AIC_{c0} – AIC_c of null model (intercept-only), df – degrees of freedom.

The analysis of understory vegetation species composition revealed that the RDA model constrained by the soil pH and mean defoliation was worse than the model with soil pH only (Table 5; Figure 3). This indicated that only soil pH drove species composition of vegetation. The main gradient revealed by the analysis (soil pH) was similar to the gradient of defoliation. Study plots divided the RDA space into three clusters: two of them grouped along the RDA1 axis, and a remote cluster of three plots at the bottom of the ordination space. The most numerous cluster in the left part of the RDA covered plots with higher mean defoliation, EIVs, positively correlated with soil pH.

However, FDis, seed mass, and height CWMs, higher in the second cluster, were negatively correlated with soil pH. The bottom cluster was characterized by low values of SLA CWM and high species richness, as well as high EIVs of moisture and light.

Table 3. Beta regression model of the proportion of moderately and severely damaged *Fraxinus excelsior* trees within sets of 15 sampled trees per study plot ($n = 27$).

Term	Estimate	SE	Z	Pr(>|z|)
(Intercept)	−3.023	0.948	−3.188	0.001
Soil pH	0.417	0.157	2.649	0.008
Soil organic matter	0.074	0.041	1.805	0.071
Precision parameter φ	10.757	2.814	3.823	<0.001
Pseudo-R^2	logLik	AICc	$AICc_0$	df of residuals
0.496	15.483	−21.148	−8.123	23

Abbreviations: SE – standard error, Z – empirical test statistic, Pr(>|z|) – p-value, based on comparison of empiric and tabular Z, logLik – log-likelihood, AIC_c – model's Akaike's Information Criterion corrected for small sample size, AIC_{c0} – AIC_c of null model (intercept-only), df – degrees of freedom.

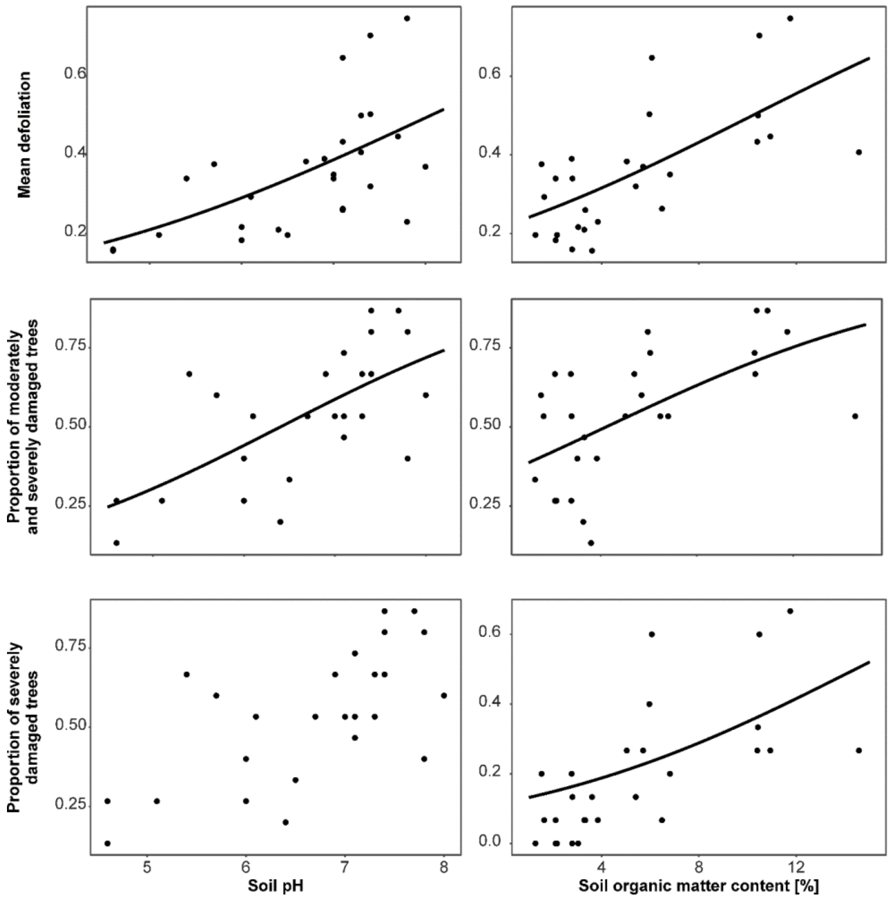

Figure 2. Relationships between soil pH (left side) and organic matter content (right side), and defoliation of *Fraxinus excelsior* (expressed as mean defoliation, proportion of moderately and severely damaged trees, and severely damaged trees only, based on 15 sample trees per study plot; upper, middle and lower rows, respectively), modeled using beta regression (Tables 2 and 4, $n = 27$). In case of relationship between soil pH and proportion of severely damaged trees we did not draw line, as soil pH was not included in final model.

Table 4. Zero-inflated beta regression model of the proportion of severely damaged *Fraxinus excelsior* trees within sets of 15 sampled trees per study plot (n = 27).

Table	Estimate	SE	T	Pr(>|t|)
μ estimation, link function: logit (Intercept)	−2.024	0.308	−6.581	<0.001
Soil organic matter	0.140	0.040	3.503	0.002
σ estimation, link function: logit (Intercept)	2.221	0.279	7.970	<0.001
ν estimation, link function: log (Intercept)	−1.482	0.495	−2.991	0.006
Pseudo-R^2	logLik	AICc	$AICc_0$	df of residuals
0.299	3.091	3.636	10.453	23

Abbreviations: SE – standard error, T – empirical test statistic, Pr(>|t|) – p-value, based on comparison of empiric and tabular T, logLik – log-likelihood, AIC_c – model's Akaike's Information Criterion corrected for small sample size, AIC_{c0} – AIC_c of null model (intercept-only), df – degrees of freedom.

Table 5. PERMANOVA test of the influence of soil pH and mean defoliation on understory vegetation species composition in redundancy analysis (RDA) in a reduced space (Figure 3). AIC_0 refers to the null model (unconstrained analysis). AIC, Akaike information criterion.

Hypothesis	Term	df	Variance	F	Pr(>F)
Impact of soil pH and defoliation	Soil pH	1	0.07848	5.4243	0.001
	Mean defoliation	1	0.02216	1.5662	0.079
	Residual	25	0.33954	-	-
	AIC	−24.18	AIC_0	−24.48	-
Impact of soil pH only	Soil pH	1	0.07848	5.4243	0.001
	Residual	25	0.36170	-	-
	AIC	−21.174	AIC_0	−24.48	-

Abbreviations: df – degrees of freedom, F – empirical test statistic, Pr(>|F|) – p-value, based on comparison of empiric and tabular F.

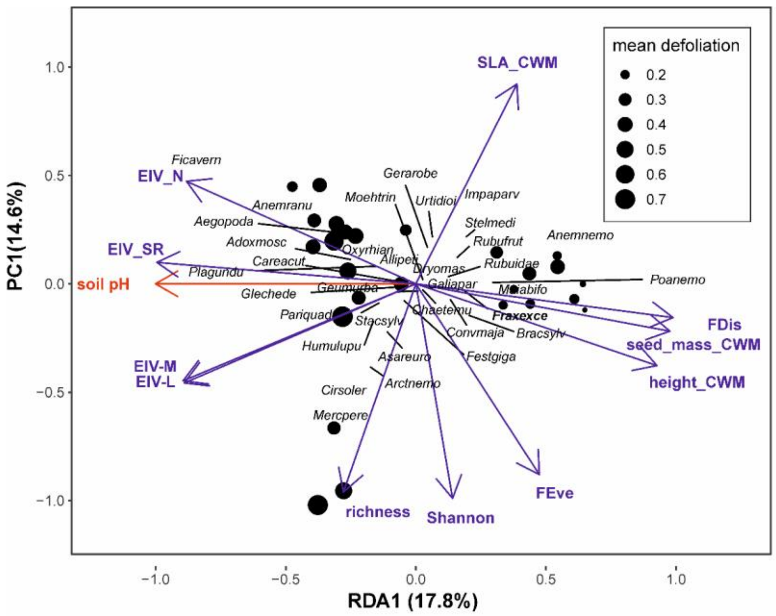

Figure 3. Results of redundancy analysis (RDA) of understory species composition at the background of mean defoliation within the study plots. Each point represent a study plot (n = 27), black names represent species scores (first four letters of genera and species name; for clarity, only species with total cover >20% were plotted; all plant species names are given in the Material and methods section). The red label indicates the constraining factor, soil pH (driver of species composition; goodness of fit test in Table 5), while blue labels indicate passively fitted vegetation features (i.e., correlated with species composition gradients; Table 6 for abbreviation and goodness of fit).

Table 6. Goodness of fit of passive projection of species composition to RDA result (Figure 3).

Variable	Abbreviation	RDA1	PC1	r^2	Pr(>r)
Ecological indicator value—light	EIV_L	−0.894	−0.447	0.255	0.033
Ecological indicator value—moisture	EIV_M	−0.889	−0.457	0.748	0.001
Ecological indicator value—soil reaction	EIV_SR	−0.995	0.099	0.815	0.001
Ecological indicator value—soil fertility	EIV_N	−0.881	0.473	0.710	0.001
CWM of height	height_CWM	0.926	−0.377	0.502	0.002
CWM of specific leaf area	SLA_CWM	0.388	0.922	0.455	0.003
CWM of seed mass	seed_mass_CWM	0.976	−0.219	0.476	0.001
Functional evenness	FEve	0.474	−0.880	0.269	0.030
Functional dispersion	FDis	0.988	−0.156	0.260	0.028
Species richness	Richness	−0.278	−0.961	0.118	0.251
Species diversity (Shannon index)	Shannon	0.141	−0.990	0.358	0.008

CWM, community-weighted mean; r^2 and p calculated using permutation tests with 999 iterations; RDA1 – coordinates of variables along the first constrained axis RDA1, PC1 – coordinates along first unconstrained axis PC1, PR(>r) – p-values of correlations between ordination and variables.

4. Discussion

4.1. Impact of soil pH and SOM Content on Crown Defoliation

The results of our study show that ash crown defoliation is correlated with the soil pH and SOM content in the A horizon. The crown defoliation was the highest in soils with pH > 7.0, and with a high SOM content (>7.5%). Such soils correspond with fertile, moist, and calcareous sites where, according to Dobrowolska et al. ash finds optimal growth conditions [35]. These sites are highly dependent on soil moisture and especially vulnerable to decreases in the groundwater table level which affects the soil pH [63]. It particularly concerns the moist sites susceptible to changes in soil moisture. This is in accordance with studies conducted in Latvia, revealing the high damage of ash stands mostly in mineral soils with decreased pH and lower Ca contents. The authors stated that the decrease in soil moisture could negatively affect trees in the research sites [31]. Our results are also in one line with recently conducted studies by Chumanová et al. who determined that the fertile lowlands and humid areas bordering Poland and Slovakia were the most endangered regions for ash disease. Areas at the lowest risk of damage were concentrated in dry areas and in highland and mountain areas in the western part of the country, usually with poor soils on acid bedrock [30].

In our study, ash crown defoliation was significantly lower within the plots with lower SOM contents, and at the same time with higher soil acidity in the A horizon. Such results were found mostly in mesic sites, which are less susceptible to fluctuations in soil moisture. It suggests that changes in soil moisture may increase tree stress, and thus the susceptibility to external factors. This is in accordance with Schütt's hypothesis [64], which states that forest tree dieback is also the result of disturbances in the functioning of fine roots and mycorrhizae because of water stress. However, in mesic sites, the soil moisture usually remains low and constant. The groundwater level is below the range of the fine roots; therefore, ash draws moisture from the atmospheric air supplied from adjacent water reservoirs. Additionally, in such sites, the density of fine roots (up to 15 cm) significantly increases [65]. In such mesic soils, water stress does not affect trees and may also impede the growth of fungal disease.

Studies conducted in northern Germany revealed that the forest type was the most important significant predictor of adult ash crown defoliation [38]. The highest proportion of damaged trees was found in wet alder-ash forests, while the lowest in ash-rich beech forests and hornbeam-ash forests [38]. However, the study did not show significant effects of chemical soil parameters on ash defoliation. This might be connected with the long environmental gradient used in this study and discontinuity among studied types of ecosystems. In contrast, our approach covered forest types sharing more common dominant tree species, comprising the usual toposequences along the moisture gradients in wetland and floodplain landscapes [66–68]. This is partly in accordance with our results. We noted the highest proportion of moderately and severely damaged trees in the plots located within the moist sites, which correspond to moist broadleaved forests, floodplain forests, and alder-ash forests (with alkaline and neutral soil pH).

Our results indicate that soil may indirectly affect ash defoliation by the promotion or inhibition of fungus development because of moisture and pH variability. As *H. fraxineus* overwinters in the form of pseudosclerotia in leaf litter, its quantity and decomposition rate might be important for the spring infestation level. *F. excelsior* leaf litter decomposition can cross 50% decay during the first year, and its rate is faster in moist sites than in dry ones [69–71]. In contrast, soil pH influence differs with the biotic factor, such as the biomass composition and growth of fungi or bacteria, both in forest and agricultural soils [72,73]. Fungi dominate in low pH or slightly acidic soils where the soils tend to be undisturbed [74]. Fungal growth increases with decreasing pH from 8.3 to 4.5, and decreases sharply below pH 4.5 [75]. Moreover, in moist and fertile conditions, ash dieback is also associated with a higher occurrence of other pathogens. In Denmark and Lithuania, *Armillaria* species, particularly *A. gallica* and *A. cepistipes*, were associated with declining ash trees, acting as secondary pathogens on weakened individuals [76,77]. In addition, the soilborne pathogens *Phytophthora* spp. were also suggested to be an additional ash decline agent [78]. These reports suggest that *H. fraxineus* development can be limited by lower ash leaf litter decomposition in mesic sites with more acidic soils. In fact, our results state that the lowest proportion of moderately and severely damaged trees was found in mesic and more acidic soils. Probably, such a soil reaction can be a limiting factor for the fungus only in mesic sites with stable low moisture in the topsoil. This topic requires further study to determine the detailed site requirements of the fungus *H. fraxineus.* For instance, in Latvia, the smallest symptoms of juvenile ash decline were observed also in mesic and mineral-potentially more acidic soils; more than 76% of trees were healthy. In contrast, in moist-potentially more fertile soils, the share of healthy trees was significantly smaller at 54% [32]. In general, more infected ash trees occur mostly on calcareous, organic soils, with the occurrence of a high groundwater level or moisture content [11,28–31,34,35,37].

4.2. Effect of Ash Crown Defoliation on Understory Vegetation

Understory vegetation occurrence and abundance in forest sites is influenced by the soil, climate factors, and nature of the tree canopy [79]. Different plant species also have various effects on light availability [80]. Ash canopies have higher light penetration than many other tree canopies, resulting in a greater amount of light being available to the understory vegetation. Ash dieback causes increased canopy gaps, and in the gap microsites with increased light availability, further replacement by other tree species [81–83]. The changing conditions are likely to lead to changes in the associated understory vegetation [8,84]. The same concern can be seen in sites disturbed by salvage logging. A comparison of the species composition of logged and unlogged sites in Białowieża revealed the great potential of affected sites for a spontaneous recovery toward light-demanding species [85].

In our study, the highest defoliation was found in neutral to slightly alkaline soils with higher SOM contents: Phaeozems, Gleyosols, and Fluvisols. Such sites usually have high species richness, soil fertility, and soil moisture [86]. Indeed, the EIVs showed that such plots were characterized by high species richness, as well as high soil fertility and moisture. However, the results of studies conducted in Germany did not show a significant effect of adult tree crown defoliation on the species richness in alder-ash forests, ash-beech forests, and hornbeam-ash forests [38]. Only the damage of juvenile ash trees was positively correlated with the total species richness; plots with a higher species richness had higher fungal damage. We assume that these differences result from the analysis of different site conditions in their study and discontinuity among the studied types of ecosystems.

We assumed that a higher EIV of light is a result of ash loss or crown defoliation that affected understory species and functional composition by increasing the proportion of competitive forest-edge species. In such plots, we noted more species typical of fertile sites, but at the same time more species with high light and moisture requirements. It is possible that their high abundance might have resulted from increased light availability, caused by ash crown defoliation that led to a shift in the understory species composition [8], as well as the composition of epiphytic lichens [7]. This resulted in a reduced functional richness and dispersion of the species composition. Within the plots with a higher crown defoliation, we found a lower proportion of the species with shade requirements, and higher proportion of species with higher light, moisture, and fertility requirements, especially tall herbs. Similar tendencies were observed in *Picea abies* Karst. forests after windthrows [87]. In contrast, we observed lower proportions of light- and moisture-demanding species in less defoliated plots, with higher CWMs of height and seed mass.

We found the highest FDis values in less fertile and more acidic soils (Cambisols, Luvisols, and Arenosols) with lower SOM contents. In such sites, we did not observe any severe ash defoliation or significant ash loss. The light conditions were also more stable, because of the lack of ash mortality-driven gaps in the overstory. Within such plots, we have noted lower EIVs of light and moisture than those in the more defoliated ash stands. Positive correlation between light and moisture requirements in riparian and wetland forests was also confirmed by Czapiewska et al. [68]. Increased cover of species with high light requirements, as well as forest edge species contributes to loss of shade-tolerant wetland specialists. In consequence, species composition of defoliated forests would resemble other vegetation types, leading to loss of vegetation distinctiveness and biotic homogenization [88].

5. Conclusions

Our study provided the first assessment of ash dieback effects (expressed by the defoliation) intensity related to soil characteristics along a continuous vegetation gradient. We found that ash crown defoliation is positively correlated with soil pH and SOM content in the A horizon. The highest proportion of moderately and severely damaged trees occurred in moist sites with high SOM contents (>7.5%) and pH (>7.0). In contrast, in mesic sites with acidic soils and lower SOM contents, we noted significantly lower crown defoliation. To identify whether these factors or other soil parameters are associated with *H. fraxineus*, it is necessary to plan more detailed further studies. In ash silviculture, we recommend, as opposed to general recommendations, to introduce ash as an admixture to mesic sites and promote its natural regeneration, even within less fertile and more acidic soils. We expect that in such conditions, ash will have a higher opportunity to survive.

Our study also revealed that the impact of ash dieback on the forest understory is indirect and unclear. Although we did not confirm the relationship between the mean defoliation level and species composition with RDA, we found more light- and moisture-demanding species in more defoliated stands. Probably, ash dieback leads to gap creation, and their colonization by other species common in these forest site, leading to a shift in the species and functional composition. Species benefiting from ash dieback are usually forest-edge tall herbs.

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