

# Variations in the population structure and ecology of *Matteuccia struthiopteris*

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**Abstract** The aim of the study was to investigate variation in the structure of a population of *Matteuccia struthiopteris* (L.) Tod. in N–E Poland depending on its location in a river valley and light availability under tree canopies. Ordination statistical methods and structural equation modeling were used to identify ecological relationships in the population. The analysis showed that optimum growth conditions of *M. struthiopteris* depend on the canopy cover. As the shading increased, the size of trophophyllous leaves and the production of sporophylls decreased. The relationship between the canopy cover and the optimum growth conditions was best expressed by rootstock diameter and, to a lesser extent, by the number and height of trophophylls. An indirect relationship between the number and height of sporophylls and the canopy cover, by rootstock size and trophophyll quantity, was also identified. This relationship may be caused by the predominance of vegetative forms of reproduction. Based on the correlations between the landscape position vs. rootstock diameter and trophophyll height, a difference in the habitat colonization potential of *M. struthiopteris* could be detected. Three spatial clusters of *M. struthiopteris* in the river valley were identified: river bank, river terrace, river valley slopes. These relationships and the distribution of other herbaceous plant species occurring at the plots indicate that the distribution pattern of *M. struthiopteris* in the study area is determined by diverse environmental conditions, however mainly by light conditions.

**Keywords** Canopy cover · Fern ecology · Landscape position · Ordination · Structural equation modelling

## Introduction

*Matteuccia struthiopteris* (L.) Tod. is widely distributed in cold temperate and boreal regions of North America and Eurasia. It occurs in areas with rich, moist soils, often on fluvial deposits (Mueller-Dombois 1964; Odland 1992). Its southern range limit intersects Poland, where *M. struthiopteris* is a protected species (Jackowiak et al. 2007). *Matteuccia struthiopteris* is listed in the *Polish Red Book of Plants* (Kaźmierczakowa and Zarzycki 2001).

Because many ferns are subject to conservation efforts, detailed information on their population dynamics is needed (Tájek et al. 2011). Studies of plant populations provide vital information regarding environmental requirements of species and their response to changes in habitat conditions. Such data are essential to evaluate the future survival of the species and to assess corrective actions in resource-management policies.

Changes in habitat conditions lead to variations in the morphological parameters of plants (Cook 1985; de Kroon et al. 1994; Ellison et al. 2004) and plant growth patterns are comprehensive indicators of environmental variation (Odland 2007). Analyses of the allocation of resources to sexual (spores or seeds) and asexual (new ramets) structures in plants provide essential knowledge on the relationships between growth and reproduction as well as on reproductive constraints in a variety of environments. Our study addresses the need to identify a conservation-friendly set of multiple factors that determine *M. struthiopteris* reproduction and growth in typical distributional

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conditions in a river valley where the influence of light under tree canopies varies.

*Matteuccia* produces separate frond rootstocks and is very well-suited for population studies. It has two distinct leaf forms: trophophylls which supply the plant with photosynthates and sporophylls, separate spore-producing leaves. Many authors have noted that since morphological traits in the populations investigated by them are susceptible to environmental changes, they play a key role in differentiating *M. struthiopteris* communities (Prange 1980; Prange et al. 1984; Prange and von Aderkas 1985; von Aderkas and Green 1986; Peck et al. 1990; Odland 1992, 1995, 2004; de Kroon et al. 1994; Kenkel 1994, 1997; Odland et al. 1998, 2004, 2006; Bergeron and Lapointe 2001; Ranker and Haufler 2008; Mehlreter et al. 2010). Favorable habitats positively affect the height, growth rate and, consequently, competitive abilities of *M. struthiopteris* (Odland 1995; Odland et al. 2004).

Research has been conducted into ecological and/or spatial variations in populations of various ferns (e.g., Watt 1974, 1976; Bartsch and Lawrence 1997; Odland et al. 2006). Odland et al. (2006) found that variations in sporophyll production of *M. struthiopteris* were correlated with the distance from the river bank, canopy cover and floristic composition of plant communities in Lithuania.

In general, the sexual organs are the most sensitive ones to environmental conditions (Pears 1985). It has been demonstrated that the ratio of sexual to asexual reproduction changes along environmental gradients (Abrahamson 1980).

The aims of our study can be formulated as follows: (1) to determine spatial distributional patterns of morphological traits of *M. struthiopteris* in a river valley and to define the main environmental gradients of the floristic composition of fern communities; (2) to investigate the structure of ecological and morphological relationships in the population: how the distance from the river and light availability under tree canopies influence the sequence of morphological growth factors such as rootstock size, the number of trophophylls and sporophylls and their height.

We also verified a hypothesis that trophophyll and sporophyll traits that are indicators of *M. struthiopteris* growth exhibit a mutually distinct model of relationships with environmental factors, mainly light conditions.

## Materials and methods

### Study area

The study area is located in the Warmia region (northeast Poland) and is fully afforested. Field investigations were carried out in a population of *Matteuccia struthiopteris*

along a 20 km long afforested section of the Lisi Parów River. The population was partly (30 %) contained within the Pióropusznikowy Jar Nature Reserve. The Lisi Parów River is a left tributary of the Bauda River and forms the hydrographic axis of the plots. It is approximately 15 km long and its catchment area is 26 km<sup>2</sup>. The Lisi Parów River intersects an isolated forest complex enclosed by farmed fields and meadows in a deep, steep erosion valley where local differences in elevation reach 50 m and the slope gradient exceeds 70° in the most extreme locations. The study area consists of largely natural riparian and beech forests which are grown for commercial purposes outside the reserve. Helocrene springs which feed other water courses in the area are a characteristic feature of the valley.

### Methods

A total of 17 plots with *M. struthiopteris*, 120–600 m<sup>2</sup> (Table 1), on both sides of the river were analyzed. A stratified random sampling method was applied. Only subpopulations where *M. struthiopteris* was dominant (more than 75 % of the cover) were selected, and the populations also had to be mature, i.e., some of the rootstocks had to be thicker than 50 mm. Similar criteria were adopted by Odland et al. (2006). The effects of population dynamics and succession should be strongly reduced in such conditions. A representative 2 m × 2 m sampling quadrat was randomly selected within each subpopulation for collection of morphological measurements, demographic data and environmental variables.

A list of species was made at the plots. Species abundances in the entire area of each of the 17 plots were estimated according to the following scale: (1) 1 %, (2) 2–5 %, (3) 6–10 %, (4) 11–25 %, (5) 26– %, (6) 51–75 %, (7) > 75 % of the cover.

Vascular plants were classified in accordance with the nomenclature proposed by Rutkowski (2004) and mosses were identified in the laboratory according to Smith (1996). Locations of the quadrats were determined with a Garmin SX60 portable GPS receiver with an accuracy of ± 3–7 m depending on the satellite signal strength. Landscape position (*Lp*) was described in meters in relation to the river and the following distance classes were accepted: (1) 0.0–0.5 m, (2) 0.5–1.0 m, (3) 1.0–1.5 m, (4) 1.5–2.0 m, (5) 2.0–2.5 m, (6) 2.5–3.0 m, (7) 4.0–5.0 m, (8) 5.0–6.0 m, (9) 6.0–7.0 m, (10) 7.0–8.0 m, (11) 8.0–9.0 m, (12) 9.0–10.0 m to the riverbed. The distance was measured from the centre of each quadrat. The diversity of the landscape position was described as follows: right/left bank, river banks (rb, limited to the borders of the riverbed, distance class: (1); river terrace (rt, riparian habitats with typical vegetation: *Ficario-Ulmetum* ash-alder streamside

**Table 1** Geographic location of the sites and quantitative data from the quadrats (Q)

Q	Size (m <sup>2</sup> )	<i>n<sub>r</sub></i>	<i>mh<sub>t</sub></i> (cm)	<i>mn<sub>t</sub></i>	<i>mh<sub>s</sub></i> (cm)	<i>md<sub>r</sub></i> (cm)	<i>maxd<sub>r</sub></i> (cm)	<i>n<sub>60</sub></i>	<i>n<sub>120</sub></i>	<i>m<sub>s</sub></i>	<i>n<sub>f</sub></i>	<i>d<sub>2</sub></i> (cm)	<i>d<sub>10</sub></i> (cm)	<i>F</i> %	<i>mLp</i> <sup>a</sup>	<i>Can</i> (%)
1_oNRd rt	200	18	113.5	9.5	48.2	54.6	100	1	3	6	5	1	2	27.8	4	10
2_oNRd rt	120	19	110.4	9.6	47.2	54.2	99	1	2	5	4	0	2	26.3	4	50
3_oNRd rv	220	21	122.5	9.7	49.3	77.2	104	1	2	3	3	0	2	14.3	8	35
4_oNRd rb	180	12	92.2	6.4	46.3	50.3	98	2	0	3	3	0	0	25.0	1	35
5_oNRd rv	320	22	127.2	10.2	52.3	80.2	120	0	4	6	4	0	4	18.2	9	35
6_oNRd rv	280	19	117.7	7.6	49.5	74.3	112	2	2	4	4	1	2	21.1	9	45
7_NR rv	360	23	139.2	10.6	57.5	84.6	119	0	12	12	8	0	6	34.8	8	35
8_NR rv	330	22	138.5	10.1	56.9	80.9	120	0	19	16	8	0	5	36.4	8	40
9_NR rv	310	19	118.2	8.3	50.3	62.0	96	3	6	4	4	1	0	21.1	8	60
10_NR rt	190	17	102.8	7.9	44.3	60.2	96	3	0	3	3	1	0	17.6	4	65
11_NR rb	160	11	100.2	5.6		59.2	91	0	1	0	6	0	0	0.0	1	50
12_oNRu rv	340	22	108.2	8.1		61.9	92	2	2	0	0	0	0	0.0	8	55
13_oNRu rv	380	25	98.4	7.6	42.0	60.5	90	5	0	10	8	0	0	32.0	8	50
14_oNRu rv	600	24	88.8	6.0		50.3	89	0	0	0	0	0	0	0.0	10	60
15_oNRu rt	230	17	64.2	5.8		46.2	80	9	0	0	0	0	0	0.0	10	75
16_oNRu rb	120	13	88.0	5.8	38.5	52.3	86	6	0	2	2	0	0	15.4	1	55
17_oNRu rt	190	16	72.2	6.2		50.1	82	6	0	0	0	0	0	0.0	3	90
Mean		19	106.7	7.9	48.5	62.3	98	2	3	4	4	0	1	17.1	6	49.7
SD		4	21.9	1.8	5.5	12.4	13	3	5	5	3	0	2	12.9	3.3	18.2

With the exception of the landscape position, entry data after a study by Grzybowski and Juśkiewicz–Swaczyna (2013)

*NR* nature reserve, *oNRd* off-nature reserve downstream, *oNRu* off-nature reserve upstream, *rb* river bank, *rt* river terrace, *rv* river valley slopes. Size = Estimated population size in m<sup>2</sup>; morphological traits in the squares: *n<sub>r</sub>*, number of rootstocks, *mh<sub>t</sub>* mean trophophyll height, *mn<sub>t</sub>* mean number of trophophylls, *mh<sub>s</sub>* mean sporophyll height, *md<sub>r</sub>* mean rootstock diameter, *maxd<sub>r</sub>* maximum rootstock diameter, *n<sub>60</sub>* number of rootstocks with trophophylls shorter than 60 cm, *n<sub>120</sub>* number of rootstocks with trophophylls taller than 120 cm, *m<sub>s</sub>* total number of sporophylls in squares, *n<sub>f</sub>* total number of fertile rootstocks, *d<sub>2</sub>* number of rootstocks with the diameter smaller than 2 cm, *d<sub>10</sub>* number of rootstocks with the diameter greater than 10 cm, *F* % the percentage of sporophyll-producing rootstocks, *mLp* mean landscape position, *Can* canopy cover

<sup>a</sup> Distance class: 1 0.0–0.5 m, 2 0.5–1.0 m, 3 1.0–1.5 m, 4 1.5–2.0 m, 5 2.0–2.5 m, 6 2.5–3.0 m, 7 4.0–5.0 m, 8 5.0–6.0 m, 9 6.0–7.0 m, 10 7.0–8.0 m from the riverbed

forests; located predominantly within 2–3 m from the riverbed borders, distance classes 2–6); and river valley slopes (*rv*, outside the river terrace, up to 10 m from the riverbed, mainly with the *Galio odorati-Fagetum* beech wood habitat—outside river terrace, maximum 10 m from the riverbed, mainly with the *Galio odorati-Fagetum* beech wood habitat; distance classes 7–12).

The abundance of each vascular plant and moss species was measured and the total cover of canopy layers was estimated visually (%). Canopy cover was estimated separately for the 17 plots (*mCan*) and the quadrats (*Can*). Plant species, additionally identified at individual 17 plots, were estimated using two indicators: substrate moisture *F* and trophy *N*. Substrate moisture (*F*) was measured on a scale of 1–12 from extreme dryness to under water; trophy (*N*) was measured on a scale of 1–9 from the poorest to extremely rich (Ellenberg et al. 1991). These measurements allowed on estimation of weighted average values for soil moisture and soil nitrogen in the plots. The individual floristic composition was characterized by following

estimates: minimum, maximum, median, mean absolute deviation. Due to a broad ecological amplitude, some species cannot be considered as indicator species of certain habitat factors (they are marked with *x* by Ellenberg et al. 1991) and they were excluded from the analysis. Six species were excluded based on substrate moisture (*F*) and five based on trophy (*N*).

*Matteuccia struthiopteris* is a clonal plant and all rootstocks within a population may represent the same genome. We investigated morphological and quantitative traits of various rootstocks within the samples, aimed at exploration of the structure of ecological and morphological relationships in *M. struthiopteris* populations. *Matteuccia struthiopteris* produces both fertile (sporophyll) and sterile (trophophyll) leaves. The following morphological traits of the rootstock were estimated: number of trophophylls (*n<sub>t</sub>*), number of sporophylls of rootstock (*n<sub>s</sub>*), sporophyll height (*h<sub>s</sub>*), trophophyll height (*h<sub>t</sub>*) and rootstock diameter (*d<sub>r</sub>*). The following variables were measured at each quadrat: number of rootstocks (*n<sub>r</sub>*), mean trophophyll height (*mh<sub>t</sub>*),

mean number of trophophylls ( $mn_t$ ), mean sporophyll height ( $mh_s$ ), mean rootstock diameter ( $md_r$ ), maximum rootstock diameter ( $maxd_r$ ), number of rootstocks with trophophylls shorter than 60 cm ( $n_{60}$ ), number of rootstocks with trophophylls taller than 120 cm ( $n_{120}$ ), number of sporophylls ( $n_s$ ), total number of fertile rootstocks ( $n_f$ ), number of rootstocks with the diameter smaller than 2 cm ( $d_2$ ), number of rootstocks with the diameter greater than 10 cm ( $d_{10}$ ), the percentage of sporophyll-producing rootstocks ( $F\%$ ), mean landscape position ( $mLp$ ) and canopy cover in plots ( $mCan$ ).

## Statistical analyses

### Detrended correspondence analysis (DCA)

DCA was used to identify the main environmental gradients that determine the vegetation structure in relation to the riverbed. Factors that mainly influence cluster formation can be identified a posteriori (based on species differences) in the analysis and the distance between clusters reflects their variation (Jongman et al. 1995; Lepš and Šmilauer 2003). The floristic composition of the population at the 17 plots represents an indicative environmental explanatory variable that can be correlated with the variation in the fern population structure. The DCA was performed to quantify relative differences between the plots based on their total species composition.

DCA axes of 1–4 sample scores were included as floristic explanatory variables. Floristic data for the DCA were collected at 17 plots. Data regarding the *M. struthiopteris* population were supplementary and were determined for the 17 quadrats that are part of the 17 plots. The functional importance of the DCA in our study is to identify the main environmental gradients that determine the vegetation structure comprising the *M. struthiopteris* population in relations to the riverbed. They were used in the DCA as supplementary variables. The mean landscape position ( $mLp$ ) was the mean value for each of the 17 quadrats and the canopy cover was estimated for the entire area of each plot ( $mCan$ ).

The following supplementary environmental variables were used in the DCA: the median of Ellenberg indicator values ( $F$ ,  $N$ ), mean landscape position ( $mLp$ ), canopy cover ( $Can$ ) and demographic and morphological traits of the *Matteuccia struthiopteris* population: number of rootstocks ( $n_r$ ), mean trophophyll height ( $mh_t$ ), mean number of trophophylls ( $mn_t$ ), mean sporophyll height ( $mh_s$ ), mean trophophyll height ( $mh_t$ ), mean rootstock diameter ( $md_r$ ), number of trophophyll-producing rootstocks shorter than 60 cm ( $n_{60}$ ), number of trophophyll-producing rootstocks taller than 120 cm ( $n_{120}$ ), number of sporophylls ( $n_s$ ), total number of fertile rootstocks ( $n_f$ ), number of rootstocks with

the diameter smaller than 2 cm ( $d_2$ ), and number of rootstocks with the diameter greater than 10 cm ( $d_{10}$ ). The relationship between ordination axes and supplementary environmental data available was examined (Jongman et al. 1995). The Pearson correlation was used as the DCA indicated that a unimodal model (gradient length 3.06 standard units) would fit the data best (ter Braak and Šmilauer 2002; Lepš and Šmilauer 2003; Piernik 2003). For Ellenberg indicator values of species representing the plots, only the relationship between the axes and the indicator values was analyzed; are presented below.

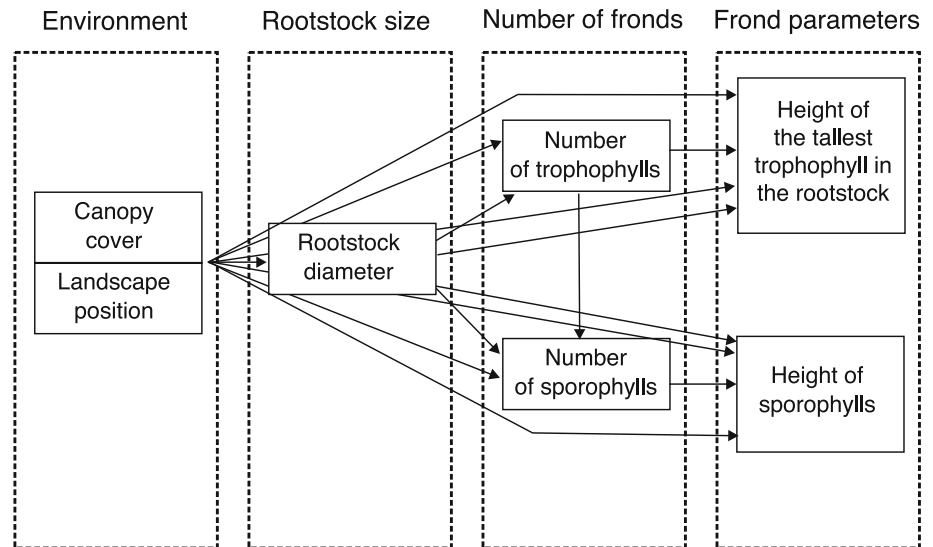
### Structural equation modeling (SEM)

Structural equation modeling, a statistical technique for evaluating causal relationships, was used to test the structure of relationships between environmental and morphological parameters in the fern population. It was done by verifying an a priori hypothesized model of these relationships with the relationships among observed variables. SEM supports the development and analysis of dependencies between variables with variation not explained in the model, and response variables (Grace et al. 2012).

There are a number of examples of ecological studies in the literature using SEM to enhance the explanatory value of the investigations. SEM approach was used in forest ecosystem nutrient cycling research (Wälder et al. 2008). Grace and Jutila (1999) showed how the grazing of the coastal grassland indirectly enhanced species diversity by reducing biomass and competition. Structural equation modelling was recently used to test hypotheses regarding evolutionary ecology of Australian *Banksia* (He 2013). As well as the above-mentioned studies, SEM modeling was also used in analyses of plant habitats by Grace and Guntenspergen (1999), Tu et al. (2000) and Sutton-Grier et al. (2010). We used SEM in our study anticipating new conclusions concerning dependencies in the ecological system of fern populations in specific environmental conditions of northern Poland. The structure of dependencies including direct and indirect sequences creates a powerful tool to assess the causal relationships among variables such as plant morphological and ecological factors (Iriondo et al. 2003).

The a priori conceptual model (Fig. 1) based on 320 *M. struthiopteris* individuals randomly selected in quadrats at 17 plots was subjected to a SEM analysis which included relationships between basic environmental features of the habitat such as the canopy cover ( $Can$ ) and landscape position ( $Lp$ ), morphological parameters represented by the rootstock diameter ( $d_r$ ), frond quantity: properties such as the number of trophophylls ( $n_t$ ) and sporophylls ( $n_s$ ), and morphological traits of the organs: the height of the tallest trophophyll in the rootstock ( $maxh_t$ ) and the height of

**Fig. 1** A conceptual scheme for the SEM path analysis demonstrating hypothesized causal relationships between environmental factors: canopy cover, landscape position; fern morphology: rootstock diameter; the number of fronds in individuals, including the numbers of trophophylls and sporophylls; and frond parameters: height of the tallest trophophyll in the rootstock, sporophyll height



sporophylls ( $h_s$ ). The model evaluated direct relationships between environmental parameters (canopy cover ( $Can$ ) and landscape position ( $Lp$ )) and the rootstock diameter ( $d_r$ ), the number ( $n_t$  and  $n_s$ ) and height ( $maxh_t$  and  $h_s$ ) of trophophylls and sporophylls, as well as direct relationships between rootstock features ( $d_r$ ) and the number ( $n_t$  and  $n_s$ ) and height ( $maxh_t$  and  $h_s$ ) of trophophylls and sporophylls. The direct influence of the number of trophophylls ( $n_t$ ) on the number of sporophylls ( $n_s$ ) was also estimated. By developing the model instead of direct relationships, the SEM analysis also identified indirect influences of environmental parameters ( $Can$  and  $Lp$ ) on frond traits realized by the rootstock size ( $d_r$ ) and by the number of trophophylls ( $n_t$ ) on its height ( $maxh_t$ ) as well as on the number and height of sporophylls ( $n_s$  and  $h_s$ ).

Before the SEM analysis, all variables were tested for the linearity of direct relationships, according to SEM acceptance of only the linear type of regression (Bollen 1989). Almost all relationships between the variables were linear, with the exception of the relationship between the landscape position ( $Lp$ ) and the rootstock diameter ( $d_r$ ) and between the number of trophophylls ( $n_t$ ) and the height of the tallest trophophyll in the rootstock ( $maxh_t$ ). The former relationship was found to be polynomial ( $y = 0.8443x^2 + 10.61x + 39.263$ ) and the latter was natural logarithmic [ $y = 47.796 \ln(x) + 11.263$ ]. To achieve linearity, the exogenous variable  $Lp$  was transformed using the polynomial regression equation and the variable  $n_t$  was transformed logarithmically. Linear transgressions of transformed variables, that were highly correlated and best accommodated for other relationships were included in the model.

In the process of evaluating an SEM of relationships between environmental and morphological traits of the population, the estimated path coefficients, i.e.,

standardized regression weights between variables, were eliminated when the regression weight for the first variable in the prediction of the second variable was significantly different from zero at  $P > 0.05$  (Arbuckle 2011). Measurement errors ( $err$ ) reflecting the variances of variables (in short: error variances) in the model were included into the analysis as unobservable variables (Arbuckle 2011). The SEM model was analyzed with the IBM® SPSS® AMOS 20.0 program. This application offers a variety of statistical tools and supports an intuitive and user-friendly presentation of SEM models in a graphic form (Byrne 2001; Iriondo et al. 2003; Walder et al. 2008). The goodness of fit of the SEM was measured using fit indices as  $\chi^2/df$  ( $\chi^2$  divided by degrees of freedom), RMSEA (Root Squared Mean Error of Approximation) and CFI (Comparative Fit Index), according to Byrne (2001) and Arbuckle (2003). The normal distribution of variables in the SEM was confirmed using the Mardia test incorporated into the analysis of the AMOS 20.0 procedure. The maximum values of skewness and kurtosis for all variables were 2.28 and 4.55, respectively, and did not exceed limits for normality proposed by Kline (2005): three for skewness and ten for kurtosis.

## Results

The fern population, flora and environmental factors relationships in a river valley

In total, 320 rootstocks were measured with 2606 trophophylls and 74 sporophylls. Morphological variation was identified for *Matteuccia struthiopteris* individuals colonizing the river section. Trophophyll height ranged from 22 to 159 cm, and ramets contained 3–22 trophophylls. An average of 5.4 rootstocks per unit of plot area with a mean



trophophyll height of 106.7 cm was recorded (Table 1). Rootstock diameter varied from 9 to 120 mm (average of 62.3 mm). Sporophyll height was determined in the range between 22 and 84 cm, but the majority of sporophylls measured from 40 to 60 cm. The tallest sporophylls were noted in ramets where trophophylls reached a height of 130–150 cm. In general, the production of *M. struthiopteris* sporophylls began upon the emergence of more than six trophophylls higher than 100 cm and when rootstock diameter exceeded 55 mm. The squares along the banks of the Lisi Parów River were characterized by a small number of new rootstocks and a high contribution of sporophyll-producing ramets (up to 36.4, 17.1 % on average) (Table 1).

Ferns at the plots occurred under tree canopy cover or under canopy gaps. The species abundances of plants at the 17 plots are presented in Table 2. A total of 52 vascular plant species and 14 moss and liverwort species were recorded at the 17 plots. The number of tracheophytes varied from 6 to 21, with an average of 12.6 plants per m<sup>2</sup>. The most frequent plants associated with *M. struthiopteris* were *Urtica dioica* L., *Aegopodium podagraria* L., *Equisetum pratense* Ehrh., *Rubus idaeus* L., *Padus avium* Mill., *Glechoma hederacea* L. and *Oxalis acetosella* L.. Bryophytes and lichens were very scarce. The species noted in the floristic composition at the 17 plots represent an incomplete range of indicators *F* (intensity 5–10) and *N* (intensity 3–8) (Table 3). A lack of indicators of minimum and maximum values of the factors is understandable due to the type of the habitats.

DCA with the demographic data introduced as supplementary variables is shown in Fig. 2. The DCA ordination showed that the lengths of the two main DCA axes were 3.06 and 1.55 SD units, and the eigenvalues were 0.58 and 0.47, respectively. The other axes are less significant. The first and second axes explained 27.7 and 12.1 % of the variation, respectively. When the environmental variables were included, axes 1 and 2 explained 28.2 and 17.6 % of the relationship between the species and the environment.

DCA axis 1 was most correlated with substrate moisture (*F*,  $r_P = 0.85$ ,  $P = 0.002$ ) and trophy indicator (*N*,  $r_P = 0.78$ ,  $P = 0.001$ ). High correlation values were detected between axis 1 and landscape position ( $mLp$ ,  $r_P = -0.64$ ,  $P = 0.006$ ), number of rootstocks ( $n_r$ ,  $r_P = -0.69$ ,  $P = 0.002$ ); mean height of trophophyll ( $mh_t$ ,  $r_P = -0.57$ ,  $P = 0.016$ ), mean rootstock diameter ( $md_r$ ,  $r_P = -0.65$ ,  $P = 0.005$ ) and the number of sporophylls ( $n_s$ ,  $r_P = -0.50$ ,  $P = 0.04$ ). DCA axis 2 was correlated only with one environmental variable: canopy cover ( $mCan$ ,  $r_P = 0.63$ ,  $P = 0.007$ ). High correlation values were detected with the mean number of trophophylls ( $mn_t$ ,  $r_P = -0.58$ ,  $P = 0.014$ ) (Fig. 2). Three axis 1 clusters can be identified on the diagram (Fig. 2). River terrace and river bank plots are clustered on the right side of the diagram;

river valley slope plots are clustered on the left side of the diagram.

This ordination indicates that axis 1 may be interpreted as a gradient of moisture and trophy decreasing with the distance from the riverbed (Fig. 2).

A range of statistically significant correlations between the canopy cover ( $mCan$ ) and traits of the *M. struthiopteris* population was identified (Table 4). The analysis shows that the optimum growth conditions of *M. struthiopteris* are related to the canopy cover. Increased canopy cover ( $mCan$ ) caused reduced sporophyll production ( $n_s$ ,  $r_P = -0.49$ ,  $P = 0.044$ ;  $n_f$ ,  $r_P = -0.57$ ,  $P = 0.018$ ; Table 4), mean height of trophophylls ( $mh_t$ ,  $r_P = -0.67$ ,  $P = 0.003$ ; Table 4), mean sporophyll height ( $mh_s$ ,  $r_P = -0.64$ ,  $P = 0.006$ ; Table 4), new small ramets ( $d_{10}$ ,  $r_P = -0.55$ ,  $P = 0.023$ ; Table 4), and the mean number of trophophylls ( $mn_t$ ,  $r_P = -0.60$ ,  $P = 0.010$ ; Table 4). It positively influenced the number of rootstocks with trophophylls shorter than 60 cm ( $n_{60}$ ,  $r_P = 0.64$ ,  $P = 0.005$ ; Table 4).

#### Structural Equation Model of *Matteuccia struthiopteris* population environmental-morphological relationships

Two main paths of hypothesized environmental—morphological relationships in the *M. struthiopteris* population (Fig. 1), including direct and indirect relationships among variables and those describing the system of relationships in the population, could be identified in the SEM of the *M. struthiopteris* population (Fig. 3).

The first path begins at environmental parameters, landscape position (*Lp*) and canopy cover (*Can*), and runs through the rootstock diameter ( $d_r$ ) to the number of trophophylls ( $n_t$ ) and the height of the tallest trophophyll ( $maxh_t$ ). The relationships described the direct and indirect dependence of morphological traits on environmental parameters. However, relationships between rootstock diameter and habitat parameters were differentiated. The impact of the canopy cover on the rootstock size was strong (Standardized Regression Weight SRW = -0.54). In contrast, the landscape position affected rootstock diameter much more weakly (SRW = 0.15). There were also differences in the strength of morphological relationships. Rootstock diameter determined the number of trophophylls quite strongly (SRW = 0.44), but the latter parameter influenced the height of the tallest trophophyll in the rootstock to a lesser extent (SRW = 0.14) (Fig. 3). Multiple correlations of variables in the path increased from  $R^2 = 0.31$  for rootstock diameter, to  $R^2 = 0.38$  for the number of trophophylls and to  $R^2 = 0.70$  for the height of the tallest trophophyll in the rootstock (Fig. 3). There were also alternative paths indicating more direct environmental (canopy cover) and rootstock size influences on the trophophyll height. One of the stronger sequences of

**Table 2** Species abundances of plants at 17 research plots

	1_	2_	3_	4_	5_	6_	7_	8_	9_	10_	11_	12_	13_	14_	15_	16_	17_	Frequency
	oNRd	oNRd	oNRd	oNRd	oNRd	oNRd	NR	NR	NR	NR	NR	oNRu	oNRu	oNRu	oNRu	oNRu	oNRu	(%)
	rt	rt	rv	rb	rv	rv	rv	rv	rv	rt	rb	rv	rv	rv	rt	rb	rt	
<i>Matteuccia struthiopteris</i>	6	6	7	6	7	7	7	7	6	7	7	6	6	7	7	7	7	100
<i>Aegopodium podagraria</i>	4	3	4	-	1	1	1	3	3	-	-	3	3	1	-	-	3	71
<i>Urtica dioica</i>	2	1	2	-	2	2	-	2	2	-	-	2	2	1	-	-	2	65
<i>Rumex hydrolapathum</i>	2	2	2	2	2	-	-	-	-	-	2	1	-	1	-	1	-	53
<i>Hypnum cupressiforme</i>	-	-	1	-	2	2	2	2	2	-	-	1	-	1	-	-	-	53
<i>Platygyrium repens</i>	-	-	1	-	2	2	2	1	-	-	-	-	1	2	-	-	1	47
<i>Myosoton aquaticum</i>	1	1	-	2	-	-	-	-	-	1	1	-	-	-	1	1	1	47
<i>Equisetum pratense</i>	1	1	-	-	-	-	-	-	-	1	1	-	-	-	1	1	1	41
<i>Alnus glutinosa</i>	2	2	-	-	-	-	-	-	-	5	4	-	-	-	4	2	4	41
<i>Corylus avellana</i>	-	-	2	-	2	4	2	2	-	-	-	2	-	2	-	-	-	41
<i>Oxalis acetosella</i>	-	-	1	-	1	1	2	1	-	-	-	-	2	1	-	-	-	41
<i>Aconitum variegatum</i>	-	2	-	-	-	-	-	-	-	2	2	-	-	-	2	2	2	35
<i>Glechoma hederacea</i>	-	-	1	-	4	-	1	2	-	-	-	2	2	1	-	-	-	35
<i>Rubus idaeus</i>	-	-	2	-	2	2	-	-	-	-	-	2	2	2	-	-	-	35
<i>Fagus sylvatica</i>	-	-	-	-	-	4	5	5	5	-	-	4	5	-	-	-	-	35
<i>Berula erecta</i>	-	-	-	2	-	-	-	-	-	-	1	2	1	2	-	1	-	35
<i>Brachythecium rivulare</i>	-	-	-	4	-	-	-	-	-	4	4	-	-	-	4	4	4	35
<i>Brachythecium rutabulum</i>	2	-	-	2	-	-	-	-	-	2	2	-	-	-	2	-	2	35
<i>Nasturtium officinalis</i>	2	2	-	2	-	-	-	-	-	1	-	-	-	-	1	-	1	35
<i>Chaerophyllum aromaticum</i>	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	1	1	29
<i>Solanum dulcamara</i>	2	2	-	-	-	-	-	-	-	2	-	-	-	-	3	-	1	29
<i>Ulotia crispata</i>	-	-	1	-	1	1	1	-	-	-	-	-	-	1	-	-	-	29
<i>Mnium hornum</i>	2	2	-	-	-	-	-	-	-	1	-	-	-	-	2	-	1	29
<i>Plagiominium undulatum</i>	2	2	-	-	-	-	-	-	-	2	-	-	-	-	2	-	2	29
<i>Conocephalum conicum</i>	4	4	-	-	-	-	-	-	-	2	-	-	-	-	2	-	4	29
<i>Poa nemoralis</i>	1	1	-	-	-	-	-	-	-	1	-	-	-	-	1	-	1	29
<i>Impatiens parviflora</i>	-	-	4	-	2	-	-	-	2	-	-	-	-	1	-	-	-	24
<i>Anemone nemorosa</i>	-	-	-	-	-	-	2	2	-	-	-	2	4	-	-	-	-	24
<i>Asarum europaeum</i>	-	-	-	-	-	-	1	1	1	-	-	-	1	-	-	-	-	24
<i>Scutellaria galericulata</i>	1	1	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	24
<i>Veronica anagallis-aquatica</i>	-	-	-	1	-	2	2	-	-	-	-	-	-	-	-	1	-	24
<i>Veronica beccabunga</i>	-	-	1	1	-	-	1	-	-	-	-	-	2	-	-	-	-	24
<i>Phalaris arundinacea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	24
<i>Hygroamblystegium tenax</i>	1	-	-	2	-	-	-	-	-	-	1	-	-	-	-	2	-	24
<i>Deschampsia cespitosa</i>	-	-	2	-	-	-	-	-	-	-	-	2	-	2	-	-	-	24
<i>Padus avium</i>	1	2	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	18
<i>Neottia nidus-avis</i>	-	-	-	-	-	2	1	-	-	-	-	1	-	-	-	-	-	18
<i>Daphne mezereum</i>	-	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	18
<i>Fraxinus excelsior</i>	-	-	-	-	-	-	-	-	-	2	-	-	-	-	2	-	2	18
<i>Scrophularia nodosa</i>	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	0	2	18

Table 2 continued

	1_ oNRd rt	2_ oNRd rt	3_ oNRd rv	4_ oNRd rb	5_ oNRd rv	6_ oNRd rv	7_ NR rv	8_ NR rv	9_ NR rv	10_ NR rt	11_ NR rb	12_ oNRu rv	13_ oNRu rv	14_ oNRu rv	15_ oNRu rt	16_ oNRu rb	17_ oNRu rt	Frequency (%)
<i>Scrophularia umbrosa</i>	1	2	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	18
<i>Quercus robur</i>	-	-	2	-	-	-	-	-	2	-	-	2	-	-	-	-	-	18
<i>Hydrohyppnum luridum</i>	-	-	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	18
<i>Wamstorfia exannulata</i>	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	18
<i>Leptodictyum riparium</i>	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	18
<i>Dicranum scoparium</i>	2	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	18
<i>Circaea lutetiana</i>	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12
<i>Platanthera bifolia</i>	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	12
<i>Actaea spicata</i>	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	12
<i>Cardamine flexuosa</i>	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	12
<i>Lysimachia thysiflora</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	12
<i>Campanula latifolia</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
<i>Hydrohyppnum luridum</i>	4	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	6
<i>mCan</i>	10	45	35	40	35	45	35	40	60	60	50	55	45	60	70	60	90	

Species abundances at each plot were estimated according to the following scale: 1 1%, 2 2–5%, 3 6–10%, 4 11–25%, 5 26–50%, 6 51–75%, 7 > 75% of the cover  
 NR nature reserve, oNRd off-nature reserve downstream, oNRu off-nature reserve upstream, rb river bank, rv river terrace, mCan canopy cover at plots

impact runs from light conditions and landscape position to rootstock diameter and directly to the height of the tallest trophophyll (SRW = 0.53). Another alternative path includes the influence of the canopy cover on the number of trophophylls (SRW = 0.26) and by this on trophophyll height, as well as the direct impact of the canopy cover on the height of the tallest trophophyll in the rootstock (SRW = 0.30) (Fig. 3). The paths between environmental parameters, mainly the canopy cover, and height properties of trophophylls were characterized by a diversity of relationships, including one or two indirect variables (rootstock size and/or number of trophophylls), as well as by direct relationships.

The second path also ran from environmental parameters to rootstock diameter and to the number of trophophylls and then to the number of sporophylls and further to the mean sporophyll height. The influence of the trophophyll quantity on the number of sporophylls was weak but (SRW = 0.18) statistically significant and the multiple correlation coefficient for number of sporophylls was low ( $R^2 = 0.03$ ). The relationship between the number of sporophylls and their mean height was very strong (RSW = 0.84) and the multiple correlation of this parameter was as high as for trophophylls ( $R^2 = 0.70$ ) (Fig. 3). The path between environmental parameters and the mean height of sporophylls was characterized by several relationships. It included two or three indirect variables such as the rootstock diameter, the number of trophophylls and the number of sporophylls. However, the relationship between the two latter parameters was not very strong.

The SEM technique supports analyses of the direct and indirect impact of variables in an SEM. Standardized regression weights between the canopy cover and the height of the tallest trophophyll in the rootstock ( $maxh_t$ ) were characterized by the highest indirect effect (−0.36). The indirect effect of the canopy cover on the number of trophophylls (−0.24) should also be noted. The height of sporophylls depended on the largest number (4) of indirect variables (Table 5).

**Discussion**

Relationships between the flora, the population structure of *M. struthiopteris* and environmental variables in a river valley

The growth, development and morphology of *M. struthiopteris* were extensively described by Prange et al. (1984), Prange and von Aderkas (1985), von Aderkas and Green (1986), Odland (1995, 2004) and Odland et al. (2006). The optimum habitat for *M. struthiopteris* is



**Table 3** Statistical properties for Ellenberg's indicator (Ellenberg 1991) values from the plots

Indicator value	Statistics	Plots								
		1_oNRd rt	2_oNRd rt	3_oNRd rv	4_oNRd rb	5_oNRd rv	6_oNRd rv	7_NR rv	8_NR rv	9_NR rv
Moisture <i>F</i>	Min	6.0	5.0	5.0	8.0	5.0	5.0	5.0	5.0	5.0
	Max	10.0	10.0	10.0	10.0	10.0	9.0	10.0	8.0	8.0
	Median	8.0	8.0	6.5	9.5	6.0	6.0	6.0	6.0	5.0
	MAD	1.4	1.3	1.6	0.8	1.3	1.3	1.8	0.7	0.8
Trophy <i>N</i>	Min	3.0	3.0	3.0	6.0	3.0	5.0	5.0	5.0	5.0
	Max	8.0	8.0	8.0	7.0	8.0	8.0	8.0	8.0	8.0
	Median	7.0	7.0	6.5	7.0	6.5	6.5	6.0	7.0	6.5
	MAD	1.1	1.1	1.0	0.4	1.1	1.0	0.8	0.8	1.0

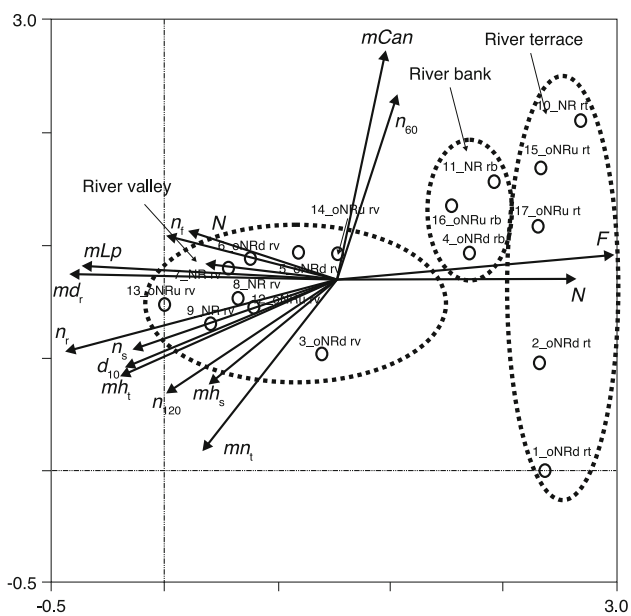
Indicator value	Statistics	Plots								
		10_NR rt	11_NR rb	12_oNRu rv	13_oNRu rv	14_oNRu rv	15_oNRu rt	16_oNRu rb	17_oNRu rt	
Moisture <i>F</i>	Min	6.0	7.0	6.0	5.0	5.0	5.0	6.0	5.0	
	Max	10.0	10.0	10.0	10.0	10.0	10.0	10.0	10.0	
	Median	8.0	8.0	6.5	6.0	6.5	8.0	8.5	7.5	
	MAD	0.8	1.1	1.5	1.6	1.4	1.2	1.1	1.2	
Trophy <i>N</i>	Min	4.0	3.0	3.0	5.0	3.0	3.0	6.0	3.0	
	Max	8.0	8.0	8.0	8.0	8.0	8.0	8.0	8.0	
	Median	7.0	7.0	6.5	6.5	6.5	7.0	7.0	7.0	
	MAD	1.2	1.3	1.3	0.8	1.1	1.5	1.1	1.5	

Min - minimum; Max - maximum; MAD - mean absolute deviation

nutrient-rich soil with base saturation optima between 56 and 64 % and the optimum water content is 42.8 % (Odland et al. 1998; Aarrestad 2002). The northern limit of its range is probably determined by summer temperature limits, but factors which affect its distribution patterns in southern regions are more difficult to identify (Prange and von Aderkas 1985). More effective protection measures can be introduced when interrelations between reproduction features and environmental features that threaten its occurrence have been explored more extensively.

Quantitative data revealed variations among individual quadrats in the *M. struthiopteris* population. The quadrats along the Lisi Parów River were mostly colonized by large plants, but plant density was low (an average of 5.4 rootstocks per unit of plot area with a mean trophophyll height of 106.7 cm). These values also indicate unfavorable humidity conditions in the plant's habitat along the Lisi Parów River. To compare, an analysis of population changes in the Kulikówka nature reserve (Kołos and Wanaks 2008) showed that the plant density at shady sites was about 6.5 per m<sup>2</sup> in 2001, while it decreased to 3.4 per m<sup>2</sup> in 2004 and to 3.3 per m<sup>2</sup> in 2005. An average increase of 6.6 per m<sup>2</sup> was recorded in the plant density in a study at shady sites in the Kulikówka reserve in 2006. Fluctuations in the population size are attributed to

droughts which occurred in 2003–2004. A negative impact of water shortages on a population of *M. struthiopteris* was indicated by Kenkel (1995), who believed that plants produced fewer trophophylls and sporophylls during a dry and hot summer. The *Matteucia* fronds consist mainly of water (Odland 2004), and they are extremely sensitive to variations in soil moisture. Even a mild water stress will decrease frond elongation (Prange et al. 1984, Prange and von Aderkas 1985). This is probably the reason why the stands have been found to be restricted to soil surfaces less than 0.6–1.2 m above the stream level in mid-summer (Prange and von Aderkas 1985). The average plant density per quadrat meter in our study area is lower than that in the population in the Kulikówka reserve recorded in 2006, but it is higher than that observed in the latter in 2004 and 2005 (Kołos and Wanaks 2008) and also lower than that in the Oxbow Woods, Delta, Manitoba (Kenkel 1995). The trophophyll height is an indicator of plant age (Odland 2004). Trophophylls at the quadrats along the Lisi Parów River were generally taller than those investigated in Canada and Norway (von Aderkas and Green 1986; Odland 2004), but somewhat shorter than Lithuanian specimens (Odland et al. 2006). The mean rootstock density of *M. struthiopteris* in Canada was eight to ten (Kenkel 1997) with a mean trophophyll height of 90 cm (von Aderkas and



**Fig. 2** A scatterplot showing the location of 17 quadrats relative to DCA axes 1 and 2. The quantitative and morphological traits variables are plotted as supplementary vectors. *NR* nature reserve, *oNRd* off-nature reserve downstream, *oNRu* off-nature reserve upstream, *rb* river bank, *rt* river terrace, *rv* river valley. Quantitative and morphological traits:  $n_r$  number of rootstocks,  $mn_t$  mean number of trophophylls,  $mh_s$  mean sporophyll height,  $mh_t$  mean trophophyll height,  $md_t$  mean rootstock diameter,  $n_{60}$  number of trophophyll-producing rootstocks shorter than 60 cm,  $n_{120}$  number of trophophyll-producing rootstocks taller than 120 cm,  $n_s$  number of sporophylls,  $n_f$  total number of fertile rootstocks,  $d_2$  number of rootstocks with the diameter smaller than 2 cm,  $d_{10}$  number of rootstocks with the diameter greater than 10 cm,  $mCan$  canopy cover in plots,  $mLp$  mean landscape position

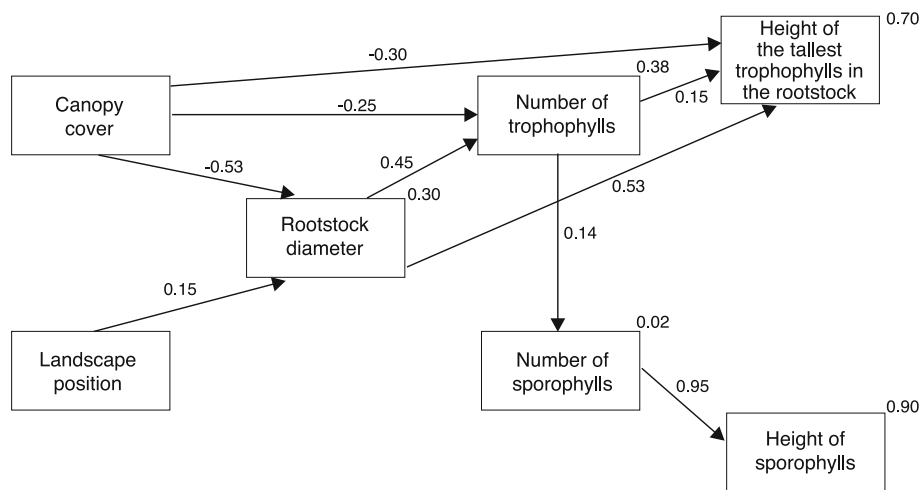
Green 1986), whereas Lithuanian populations were characterized by a mean trophophyll height of 116 cm and an average of three rootstocks per area unit (Odland et al. 2006).

The quadrats along the banks of the Lisi Parów River were characterized by a small number of new rootstocks and a high contribution of sporophyll-producing ramets (up to 36.4, 17.1 % on average, Table 1). Similar results were noted in Lithuania (Odland et al. 2006), where the populations had a small number of new rootstocks, a high percentage of sporophyll-producing ramets (up to 54.5 %) and a mean fertility rate of 14.8 %. Von Aderkas and Green (1986) found that 17 % of the plants produced sporophylls in Canada, whereas rootstock fertility in Kenkel’s study (1997) varied from 0.45 to 4.45 %. The above findings are consistent with plant behavior patterns noted along temperature gradients, which shows that plants are more likely to reproduce asexually at low temperatures (Odland et al. 2004).

The mean rootstock diameter was 62.3 mm (Table 1), which is below the values noted in Lithuania (68.7 mm) (Odland et al. 2006), but higher than those in Canada (43 mm) (von Aderkas and Green 1986). According to Prange and von Aderkas (1985) as well as von Aderkas and Green (1986), fern rootstocks have to reach a certain age or size to produce sporophylls. Developed sporophylls were rarely observed in rootstocks with a diameter smaller than 4 cm and trophophylls shorter than around 120 cm (Odland 2004). These values may be reached 3 years after rootstock formation but, even then, sporophylls are not produced

**Table 4** Intercorrelations between statistically significant environmental and morphological parameters ( $P < 0.5$ ), including DCA axes 1 and 2, at the plots with *Matteuccia struthiopteris* ( $n = 17$ )

Variables	2	3	4	5	6	7	8	9	10	11	12	13	14
DCA ax 1	1		-0.69	-0.57		-0.65	-0.50					-0.64	
DCA ax 2	2				-0.58								0.63
Number of rootstocks ( $n_r$ )	3				0.57	0.49	0.49					0.82	
Mean sporophyll height ( $mh_s$ )	4				0.71	0.59	0.71		0.65	0.60			-0.64
Mean height of trophophyll ( $mh_t$ )	5				0.87	0.88	0.71	-0.75	0.73	0.68	0.80		-0.67
Mean number of trophophylls ( $mn_t$ )	6					0.75	0.70	-0.56	0.65	0.54	0.82		-0.60
Mean rootstock diameter ( $md_t$ )	7						0.65	-0.56	0.69	0.59	0.82		
Number of sporophylls ( $n_s$ )	8								0.82	0.84	0.77		-0.49
Number of rootstocks with trophophylls shorter than 60 cm ( $n_{60}$ )	9										0.89		0.64
Number of rootstocks with trophophylls taller than 120 cm ( $n_{120}$ )	10												
Total number of fertile rootstocks ( $n_f$ )	11										0.60		-0.57
Number of rootstocks with the diameter greater than 10 cm ( $d_{10}$ )	12												-0.55
Mean landscape position ( $mLp$ )	13												
Canopy cover at plots ( $mCan$ )	14												



**Fig. 3** A structural equation model (SEM) of the correlations between environmental and morphological parameters of a *Matteuccia struthiopteris* population after the elimination of regression weights which are not significant ( $P > 0.05$ ). Boxes represent observable variables, numbers along the arrows represent

standardized regression weights of the relationship and numbers by the corner of a box signify squared multiple correlations of exogenous variables. Fit indices for the model:  $\chi^2 = 16.092$ ,  $df = 12$ ,  $\chi^2/df = 1.34$ ,  $P = 0.187$ , RMSEA = 0.033, CFI = 0.997

**Table 5** Indirect standardized regression weights of variables in an SEM analysis of environmental and morphological parameters of *Matteuccia struthiopteris*

Variables	Landscape position	Canopy cover	Rootstock diameter	Number of trophophylls	Number of sporophylls
Rootstock diameter	0.00	0.00	0.00	0.00	0.00
Number of trophophylls	0.07	-0.24	0.00	0.00	0.00
Number of sporophylls	0.01	-0.07	0.07	0.00	0.00
Height of sporophylls	0.01	-0.07	0.06	0.14	0.00
Height of the tallest trophophyll in the rootstock	0.09	-0.36	0.07	0.00	0.00

every year (Prange and von Aderkas 1985; von Aderkas and Green 1986; Kenkel 1997). A close linear correlation generally exists between the trophophyll height, rootstock diameter and sporophyll production (von Aderkas and Green 1986; Odland et al. 2006). A ramet may produce from one to nine sporophylls per year, but only 4 % of rootstocks in fertile habitats were found to produce more than six sporophylls (Odland 2004). Our results confirm that an increased number of sporophylls was correlated with an increased number and height of trophophylls at the quadrats. In general, the production of *M. struthiopteris* sporophylls began upon the emergence of more than six trophophylls higher than 100 cm and when rhizome thickness exceeded 55 mm.

Complex relationships between environmental factors were identified by Odland (2007). *Matteuccia struthiopteris* is a half-shade adapted plant (Ellenberg et al. 1991) with an Ellenberg light factor of 5. Both excessive and insufficient exposure to light could hinder optimal development of the species. Sunshine filtering through to the forest floor is modified by the canopy cover. The canopy

cover and other environmental factors also affect the amount of rainfall which reaches the forest floor. Odland (2007) believes that the canopy cover is strongly correlated with the rainfall gradient and the average January temperature. These correlations were recorded in central Norway, but they have not been confirmed in studies of *M. struthiopteris* populations in Western Europe or in western Norway.

The canopy cover varied between 10 and 90 % in our population (quadrats) and plots (Tables 1, 2). Tree and shrub canopies at some quadrats were too dense to support optimal fern growth. The plants affected by it developed short trophophylls and their sporophyll production was low. It should be noted that only 1 % of sporophyll-producing plants were found at shaded quadrats in Canada (Prange and von Adrekas 1985). A lower canopy density and greater exposure to direct sunlight seem to boost the reproductive performance of *M. struthiopteris*. A higher number of rootstocks measuring less than 2 cm in diameter was reported in areas where the canopy cover was 30 % lower in comparison with the remaining quadrats ( $t = -$

3.07,  $P = 0.003$ ). Similar results were reported by Prange and von Aderkas (1985), von Aderkas and Green (1986), and Bergeron and Lapointe (2001). A study by Kołos and Wanaks (2008) showed that *M. struthiopteris* in the Kulikówka valley was larger in shady areas than in full sunshine. It also forms longer and broader leaves and keeps out from open spaces, occurring under the canopy of trees. The growth of *M. struthiopteris* is not favored by a sudden canopy removal; leaves turn brown and die when exposed to intensive sunshine (Bednarz 1968; Endler et al. 2006). Increased permeation of light to the forest floor as a result of reduced tree density may contribute considerably to *M. struthiopteris* receding from forest habitats (Kołos and Wanaks 2008). However, excessive shading also negatively affects its viability (Zawadzka and Zawadzki 2006). Exceptionally, plots of *M. struthiopteris* were found at sites where the density of the canopy of trees exceeded 80 % (e.g., 17\_oNRu rt; Table 1). Increased shading was accompanied by a decrease in the size of trophophylls and the production of sporophylls, which was also reported by other researchers (Odland et al. 2006; Odland 2007), with a simultaneous increase in the mean height of trophophylls and sporophylls and the maximum rootstock diameter.

The ecological amplitude of plant communities is usually narrower than that of individual species and communities are more sensitive indicators of environmental conditions (Schaffers and Sykora 2000; Diekmann 2003). Our results also confirm this as the mean indicator values for floristic composition have narrower ranges while the species noted by us have a broad range of indicators  $F$  and  $N$ .

Differences in the floristic composition of the plots along the Lisi Parów valley (DCA axes 1 and 2 are both less than 3.5 SD) indicate higher floristic variation than that in Lithuanian populations of *M. struthiopteris* (DCA axes 1 and 2 are both less than 2.7 SD units; Odland et al. 2006) and lower variation than that in Norwegian populations (DCA axes 1 and 2 are both less than 6.1 SD; Odland 2007). Indicator values ( $F$ ,  $N$ ) of species representing the plots indicate that there exist environmental gradients described by them, which is consistent with the results by Odland (1992), and they confirm the existing landscape variation of the plots. The variation in the floristic composition in the community was significantly correlated with the landscape position ( $mLp$ ,  $P = 0.006$ ), which was also observed in Lithuania (Odland et al. 2006), and which confirms that *M. struthiopteris* prefers rich alluvial sites, and is particularly common on river plain fluvial deposits (Mueller-Dombois 1964; Odland 1992; Kenkel 1997). The population of *Matteuccia struthiopteris* colonized *Ficario-Ulmetum* ash-alder streamside forests (Knapp 1942; Matuszkiewicz 1976) in the river terrace (rt) and *Galio odorati-Fagetum* lowland beech forests (Rübel 1930; Sougnez and

Thill 1959) in the river valley slopes (rv) according to phytosociological studies. Soil moisture content contributed to the fertility rate and the ability of *M. struthiopteris* to produce sporophylls was compromised in dry habitats. Riparian forests with naturally high moisture levels are the optimum habitat for *M. struthiopteris* (Grzybowski et al. 2004). The DCA analysis confirmed differentiation of morphological and quantitative traits at the localities in riparian habitats (rt), beech woods (rv) and close to the riverbed (rb) (Fig. 2).

Correlations between the landscape position ( $Lp$ ) vs. number of rootstocks ( $n_r$ ) are indicative of the differences in the habitat colonization potential of the plant (Table 4; Fig. 2). This was confirmed by findings in previous studies (Prange 1980; Prange and von Aderkas 1985; von Aderkas and Green 1986; Odland 1992, 2007; Kenkel 1997; Odland et al. 2006). Such differences have been observed in other fern species (e.g., Sheffield 1996; Flinn 2006; Mehltreter et al. 2010). There is no certainty, however, as to the cause of these differences. Svenning et al. (2008) suggest that the pattern of fern distribution in forests better explains the diversity of a glacial landscape than the patterns based on climatic or soil conditions, which is also indicated in our results. A relationship between the height of sporophylls and trophophylls (and their number) and the canopy cover was observed. Our results also indicate that the canopy cover influences the formation of new rosettes and sporophyll production (Table 4), which was also noted in Lithuania (Odland et al. 2006).

#### The structure of relationships between environmental and morphological parameters in a *Matteuccia struthiopteris* population

The use of structural equation modeling was caused by the need to enhance understanding of a natural system of variables in which habitat conditions and morphological growth factors of *Matteuccia struthiopteris* were created by a network of relationships. In SEM, path analysis can be used in ecological systems to test hypotheses with variables which can simultaneously act as predictors and outcomes (Harrison et al. 2006).

Previous studies on *Matteuccia struthiopteris* populations revealed that an increased fertility rate was correlated with direct light availability (Prange and von Aderkas 1985; von Aderkas and Green 1986; Bergeron and Lapointe 2001). The fertility rate of populations directly exposed to sunlight was higher than in populations growing under a dense canopy (Prange and von Aderkas 1985; von Aderkas and Green 1986; Bergeron and Lapointe 2001). Ostrich fern finds optimum growth conditions at a density of the canopy of upper layers of plants of 20 % (Odland et al. 2006). Our investigations confirmed these findings

and also indicate that the relationship is best expressed by the rootstock diameter ( $d_r$ ) and, to a lesser extent, by quantitative ( $n_t$ ) and morphometric ( $maxh_t$ ) traits of trophophylls. It also revealed a secondary relationship between quantitative ( $n_s$ ) and morphometric ( $h_s$ ) traits of sporophylls and the canopy cover ( $Can$ ). The occurrence of vegetative forms of reproduction may be favorable for a population affected by other factors. New plants in dense populations of *M. struthiopteris* were not formed by sexual reproduction presumably due to a strong allelopathic effect which inhibited the growth of new ramets (Prange and von Aderkas 1985; von Aderkas and Green 1986; Peck et al. 1990). Prange (1980), Prange and von Aderkas (1985), von Aderkas and Green (1986) and Kenkel (1997) noted that the production of sporophylls depended on plant age. Their findings show that a rootstock must achieve a certain age or size before it can produce sporophylls (Odland 2004). Such factors can explain an indirect relationship between environmental factors, canopy cover and landscape position, and sporophyll traits ( $n_s$ ,  $h_s$ ) in the population of *M. struthiopteris*, investigated in a structural equation model (Fig. 3).

## Conclusions

Light availability (canopy cover) and substrate moisture identified using the floristic composition with Ellenberg values are the most important factors that determine the distribution pattern of *M. struthiopteris* in the study area. Three spatial clusters of *M. struthiopteris* in the river valley were detected in the DCA: river bank, river terrace, river valley slopes.

Increased light availability at the plots positively influences the production and height of trophophylls and sporophylls while increased shading may inhibit the growth of new trophophylls.

Using structural equation modeling, we confirm the initial hypothesis that trophophyll and sporophyll traits that are indicators of *M. struthiopteris* growth exhibit a mutually distinct model of relationships with environmental factors, mainly light conditions.

The number of trophophylls and their height directly depends on the availability of light and landscape position (to a lesser extent) as well as indirectly by rootstock size.

The number of sporophylls and their height shows direct relationship with rootstock size and trophophyll quantity and indirect relationship with environmental parameters, probably resulting from the predominance of the vegetative form of reproduction in *M. struthiopteris*.

Analysis of the distribution of basic growth traits of *M. struthiopteris* in a river valley and the analysis of the

relationships between environmental and morphological factors should contribute to a better understanding of the ecological relationships of the species and its protection, mostly by managing light availability through canopy cover.

The use of the analysis of the spatial distribution based on the floristic composition (DCA) along with the analysis of the relationship between the environment and growth parameters (SEM) gives a fuller image of their population ecology.

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