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Distribution of vascular plant species in woodland patches of Ojców National Park (southern Poland) in relation to seed dispersal

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Abstract

Plant diaspore dispersal is a fundamental process affecting the development of forest vegetation and its natural regeneration, especially with regard to typical woodland species, which spread slowly and form short-term soil seed banks. Most of these species have poor seed dispersal mechanisms, which is the major cause of their very slow expansion.

The following questions were asked: (*i*) is there a relationship between the age of a woodland and the presence of forest vascular plant species representing different seed dispersal types; (*ii*) how do the proportions change between species representing different seed dispersal types in relation to the age of woodland; (*iii*) what factors determine the presence of species representing a given seed dispersal type; (*iv*) which factors affect the presence and which ones influence the abundance of selected woodland species? A multiple regression models were developed based on data obtained from 144 woodland patches designated for the study. A probit regression analysis was performed for selected species exhibiting various seed dispersal models.

Woodland plants of all seed dispersal types show a significant relationship with the age of woodland, starting from the strongest linkage: anemochores, myrmecochores, endozoochores, epizoochores, barochores, autochores. As the woodland ages, the proportion of forest myrmecochores and anemochores grows, whilst the proportion of autochores, epizoochores and endozoochores shrinks. Results obtained indicate that the direct proximity of ancient woodland has a major effect on the occurrence of more poorly dispersing plants in recent woodlands, such as myrmecochores and heavy anemochores.

Keywords

seed dispersal; species richness; ancient woodlands; Ojców National Park; multiple regression; probit regression

Introduction

The dispersal of plant diaspores is a vital process affecting the development of woodland vegetation and its natural regeneration. It is a limiting factor for the regeneration of forest communities, particularly regarding typical woodland species that disperse slowly and form only short-term soil seed banks [1]. Given the occurrence of some species exclusively in ancient woodlands, indicator species of ancient woods can be distinguished [2,3]. Their occurrence implies the long-term presence of a forest community at a particular location, or at least a forest habitat [3]. Regional indicator species may vary, not only due to the ecological traits of these plants, but also climate-related reasons, substrate type, geological structure, and the different tolerance ranges

of ecotypic forms [3–5]. Indicator species of deciduous forests are mostly geophytes and stress-resistant species [3]. The majority of these species have poor seed dispersal mechanisms, which is the main reason of their very slow expansion [3,6,7–11].

Various studies have shown that ancient woodlands usually are much richer in forest species than recent woods (e.g., [2,3,12–14]). Secondary woodlands in Europe and Poland developed chiefly on agricultural areas, predominantly those deforested in the nineteenth century. They are marked by a different species composition and soil properties associated with the communities occurring formerly in a particular site.

In the temperate zone, post-cultivation and post-farming areas undergo succession, which eventually leads to the formation of forests. However, the regeneration of forest communities is a long and complex process [2,7,9,13,15]. Tree growth and increasing canopy density cause a large part of non-woodland species to withdraw, thus reducing the total number of species, while the subsequent colonization by forest species results in this figure rising again [16,17]. Due to the low diaspore viability of woodland species in soil, the area is usually colonized again by forest herb layer species after the recovery of the canopy layer. This process can have a local character if plants spread from the older woods to the adjacent newly-growing woods or a long-range character with the plants colonizing distant and isolated woodlands. The colonization of recent secondary woodlands proceeds slowly. They are often so slowly colonized by forest species that the restoration of a typical species composition takes several hundred years [18,19], up to 800 according to Peterken [20]. There are authors who regard that secondary woodlands can never reach the number of species present in ancient woodlands of primary origin [21].

Some researchers note that colonization is a two-stage process. The first stage is said to involve diaspores arriving in a new area and sprouting into the initial species layout [7]. The vital determinants of this process are said to include: dispersal dependent on diaspore availability and recruitment dependent on habitat conditions. The second stage is described as the species layout being modified by habitat factors and competition from other species [22,23]. A number of studies show that the diaspore availability and the age of a recent woods, as well as competition from non-woodland plants, are the major factors strongly affecting the colonization process [7,8,23–28].

Typical woodland plant species tend to produce small numbers of seeds, which is most efficient in these conditions due to their energy expenditure [29]. Their seeds are often large and have a short survival span in soil. Many of them, mainly long-lived perennials, distribute via different forms of vegetative propagation [30]. However, this method does not allow for a rapid colonization of new areas, especially those separated by open spaces. There are exceptions to this rule: rhizomes can be excavated by wild boars, roe deer, and deer. Partly eaten, they can thus be transported over large distances. The migration rate may therefore increase, reaching up to 25 meters a year. Nevertheless, this type of colonization requires soil to be transferred together with the sprout (rhizome), given the high sensitivity of these organs to drying. This example is derived from research carried out in Białowieża [31]. Longevous woodland plants, which propagate vegetatively in stable forest communities, are often incapable of generative reproduction in the event of altered conditions, e.g., as a result of canopy thinning. As a consequence, they lose out in competition with other species.

The aim of this study was to investigate: (*i*) if there is a relation between the age of a woodland and the presence of species representing different seed dispersal types; (*ii*) how the participations of species displaying different dissemination modes change in relation to the woodland's age; (*iii*) what factors affect the occurrence of selected forest species and what factors determine their abundance.

Material and methods

Study area

Ojców National Park (ONP; 50°12′24″ N 19°49′45″ E) is located in the southern part of the Kraków-Częstochowa Upland (southern Poland). It covers a part of the northern section of the Prądnik River Valley and the Sąspówka valley, the latter being a

tributary to the former [32]. The area is marked by major landform diversity resultant to water erosion. Jurassic limestone karst formations are its characteristic element [33]. This area is distinguished by steep valley slopes with numerous limestone rocks and considerable height differences. Hilltop surfaces reach a maximum altitude of 485 m above sea level. The lie of the land determines wide habitat diversity. The specific mesoclimate of this area shows many analogies to a mountain climate: longer persistence of snow cover, frequent thermal inversions, frost pockets, and higher humidity inside the valley [34].

The Park's vegetation is predominated by forests [35]. Woodland communities are varied [36–38]. Fragments of carr associations of the *Alno-Ulmion* alliance occur in valley bottoms, whereas slopes in the ONP are overgrown with beech woods represented by the following associations: *Dentario-glandulosae Fagetum*, *Carici-Fagetum convallarietosum*, and *Luzulo pilosae-Fagetum*, depending on slope exposure and habitat conditions. Sycamore woods classified as *Phyllitido-Aceretum* and *Lunario-Aceretum* associations occur on cool and less sunlit hillsides. The remaining forest communities are oak-hornbeam woods represented by the *Tilio-Carpinetum* association and *Pino-Quercetum* mixed coniferous forest associations.

Data collection and analysis

Based on various authors' findings and a detailed review of woodland vegetation occurring in the ONP, thirteen factors were selected that may have an impact on the species composition and richness of woodlands in this site, namely: area, perimeter, shape index, slope gradient, exposure, microrelief complexity, presence of rocks, age of the oldest adjacent woodland, direct contact with moist habitats, direct contact with meadows or grasslands, direct contact with agricultural used areas.

Observations were confined to the central part of the park, where the diversity of forests and their habitats is widest. It is also the location of the oldest and best-preserved woods. The study covered 144 woodland patches differing in age and uniform in terms of the selected factors, i.e., with unvaried landform features, exposure, presence of rocks, and of similar slope inclination, etc. [14] (Tab. 1).

Tab. 1 Characteristics of studied woodland patches. Explanations are provided in the text.

Number of studied woodland patches	144
Area (ares)	10–1220
Perimeter (meters)	160–3000
Shape index	1.04–2.22
Mean slope inclination (°)	0–40
Maximum slope inclination (°)	0–80
Exposure (number of woodland patches)	S (16); SW, SE (18); E, W (24), NE, NW (22); N (20), 0 (44)
Landform complexity (number of woodland patches)	0(54), 1(61), 2(29)
Presence of rocks (number of woodland patches)	0(73), 1(71)
Age of oldest adjacent forest (years)	below 71 – over 216
Contact with moist habitats (number of woodland patches)	0(103), 1(41)
Contact with meadows or grasslands (number of woodland patches)	0(86), 1(58)
Contact with agricultural used areas (number of woodland patches)	0(108), 1(36)

The age was determined using a map showing the distribution of woodlands of different ages [39]. In this paper, woodland age denotes the span of continuous existence of a forest community or at least a forest habitat at a particular location, without being even temporarily converted into arable fields or otherwise subjected to human use, save for forest management (e.g., [8,14,20,27–29,40,41]). In line with this understanding, the continuity of a woodland also remains uninterrupted in the case of a full clearance of a tree stand, provided that it has recovered via natural succession or artificial reforestation directly afterwards. The age of woodland in the investigated area is not tantamount to the age of tree stands. Secondary woods situated in hilltop zones of the area often contain exuberant and older tree stands, whereas some ancient woodlands on the slopes in the Prądnik River Valley lack exuberant old trees. This is largely due to the formerly conducted forest management and partly to the natural replacement of tree stands.

The surface areas and perimeters of studied forests or their parts were calculated from the previously developed ONP woodland-age map at a scale of 1:10 000 [39]. Shape index was computed using the formula:

$$I_S = P/2\sqrt{A\pi}$$

where P denotes perimeter, and A surface area (cf. [16]). The higher I_s value, the longer the perimeter of the studied forest relative to its surface area.

As regards the statistical analyses of exposure, the following numerical values were adopted: 0 – uninclined surface, 1 – northern facing, 2 – northeastern or northwestern facing, 3 – eastern or western facing, 4 – southeastern or southwestern facing, 5 – southern facing.

The presence of rocks, although associated with landform features, was considered a separate category describing a habitat. Landform complexity was assessed visually using the following scale: 0 – flat area, 1 – mildly undulating surface, i.e., area with slightly diverse relief, 2 – strongly undulating surface, i.e., area marked by diverse relief or featuring single deep hollows or protruding elevations (e.g., small ravine, deep depression or post-agricultural structures in the form of high balks).

Moist habitats refer to areas along watercourses – periodic or permanent flows – mainly in the Sąspów Valley, as well as some ravines and gorges. Agricultural used areas were considered to include: arable fields, orchards, outbuildings, lawns, home gardens, etc. They are mostly located in the hilltop parts of the study area and in the Prądnik River Valley. The 167 lack of contact with the mentioned areas was presented as 0, while the close proximity of 168 them as 1.

In the years 2003–2005, lists of vascular plant species occurring on each patch were compiled in different periods of the vegetation season (from April to September). Species nomenclature was consistent with Mirek et al. [42]. The abundance of species recorded was also determined according to the following scale: 1 – single individuals of the species scattered throughout the entire forest, 2 – species occurring in large numbers only in one site or in small numbers throughout the entire forest, 3 – numerous individuals of the species throughout the entire forest, 4 – a large number of individuals throughout the entire forest (the species dominates) or a large number of clusters formed by numerous individuals.

In order to investigate whether a seed dispersal mode may impact the species composition of the studied woodlands, the chief dispersal mode was determined for each recorded taxon. The species were categorized into the following groups: epizoochores, endozoochores (fleshy fruit producers), myrmecochores, dyszoochores, hydrochores, autochores, barochores (with seed weight over 3 mg), hovering anemochores (seed weight up to 0.1 mg, or up to 0.5 mg with functional flying apparatus), light anemochores (seed weight up to 0.5 mg, or up to 1.5 mg with functional flying apparatus), and heavy anemochores (seed weight up to 1.5 mg, or up to 3 mg with functional flying apparatus; cf. [43]). Species dispersal types were derived from literature.

Multiple regression was applied in data analysis to ascertain which factors significantly affected the occurrence of species representing different dispersal types in the studied woods. Independent variables in the regression model were determined using the backward stepwise method [44]. In order to establish to what extent the independent variables may have affected the number of species, standardized partial regression coefficients were calculated. The higher the coefficient, the stronger the

Tab. 2 Mean (minimum – maximum) number of herb layer species of various seed dispersal modes in the studied woodlands.

	Autochores	Anemochores	An1	An2	An3	Barochores	Epizoocores	Endzoochores	Myrmecochores	Dyszoochores	Hydrochores	Other
All woodlands	2.32 (0–5)	8.94 (1–24)	2.84 (0–9)	4.26 (0–13)	1.84 (0–6)	1.63 (0–7)	3.38 (0–10)	5.53 (0–16)	6.08 (0–16)	0.72 (0–3)	0.27 (0–2)	0.10 (0–2)
Ancient woodlands	2.97 (1–5)	14.00 (5–24)	4.61 (1–9)	6.97 (1–13)	2.42 (0–6)	3.00 (0–7)	5.03 (1–10)	7.42 (2–16)	9.91 (3–16)	1.00 (0–3)	0.52 (0–2)	0.15 (0–1)
Woodlands aged 123–216 years	2.39 (1–4)	9.41 (2–20)	2.83 (0–7)	4.34 (1–11)	2.24 (0–6)	1.51 (0–5)	3.02 (0–8)	5.83 (1–14)	6.27 (1–14)	0.76 (0–3)	0.24 (0–1)	0.07 (0–1)
Woodlands aged 71–122 years	2.11 (0–4)	7.04 (2–17)	2.30 (1–6)	3.24 (0–9)	1.50 (0–4)	1.13 (0–5)	2.74 (0–8)	4.89 (1–11)	4.91 (1–13)	0.59 (0–2)	0.24 (0–2)	0.13 (0–2)
Woodlands aged below 71 years	1.70 (0–3)	4.61 (1–15)	1.39 (0–3)	2.26 (0–8)	0.96 (0–4)	0.87 (0–3)	2.91 (0–7)	3.57 (0–9)	2.57 (0–10)	0.52 (0–2)	0	0

An1 – hovering anemochores; An2 – light anemochores; An3 – heavy anemochores.

impact of a given independent variable. The following threshold values were adopted during the selection of independent variables for their addition to or removal from the model: $F = 3.0$ and $F = 2.95$ respectively. The distributions of all quantitative independent variables were examined prior to the regression analysis. Because all distributions were symmetric or close to symmetric, and a logarithmic transformation caused no increase in their symmetry, the variables used in the regression analysis were untransformed. Dummy variables, i.e., ones that take only one of two possible values, 0 or 1, were also included in the analysis. These variables were the following four: presence of rocks, contact with moist habitats, with meadows or grasslands, and with other agricultural used areas. In order to avoid autocorrelation, the degree of correspondence between quantitative independent variables was checked via calculating the correlations between them using Pearson's coefficient. In order to exclude the impact of spatial autocorrelation, only the results of high statistical significance were taken into account ($p < 0.001$).

It was also investigated which variables were associated with the abundance of selected species in the studied woodlands. To this end, probit regression analysis with Wald's test was performed. The backward stepwise method was also employed in this case. The basic selection criterion for single species for the regression analysis was their more frequent occurrence in the studied woodlands (in at least 40). Species that showed a connection with different independent variables were selected from among those analyzed.

Results

In 144 explored woodlands, a total of 199 vascular plant species were found, including 23 trees and 9 shrubs.

In ancient woodlands there are more species in the herb layer, representing all seed dispersal types (Tab. 2). The most substantial reduction in the number of species in recent woodlands versus ancient woodlands was noted for myrmecochores and anemochores, whilst the shift was only slight in the case of autochores, epizoochores, and endozoochores.

The proportion of poorly dispersing species is larger in ancient woodlands (myrmecochores, autochores), whereas the proportion of rapidly dispersing (endozoochores, anemochores) ones is higher in secondary woodlands and its rise is more evident in the studied woodland patches, the younger the woodland is (Fig. 1).

The participation of woodland myrmecochores and anemochores grows with the advance of woodlands age, whilst that of autochores, epizoochores, and endozoochorest diminishes. The numbers of woodland plants representing all dispersal types show a significant relationship with woodland age (Tab. 3). The strongest relation has been demonstrated for anemochores and myrmecochores, followed by endozoochores, epizoochores, barochores, and autochores. The weakest relation to woodlands age is displayed by dyszoochores.

Species that can be exclusively found in ancient woodlands: *Neottia nidus-avis* (An), *Lathraea squamaria* (M), *Arum alpinum* (En), and *Phyllitis scolopendrium* (An), or both in ancient woodlands and the oldest recent ones: *Cephalanthera longifolia*
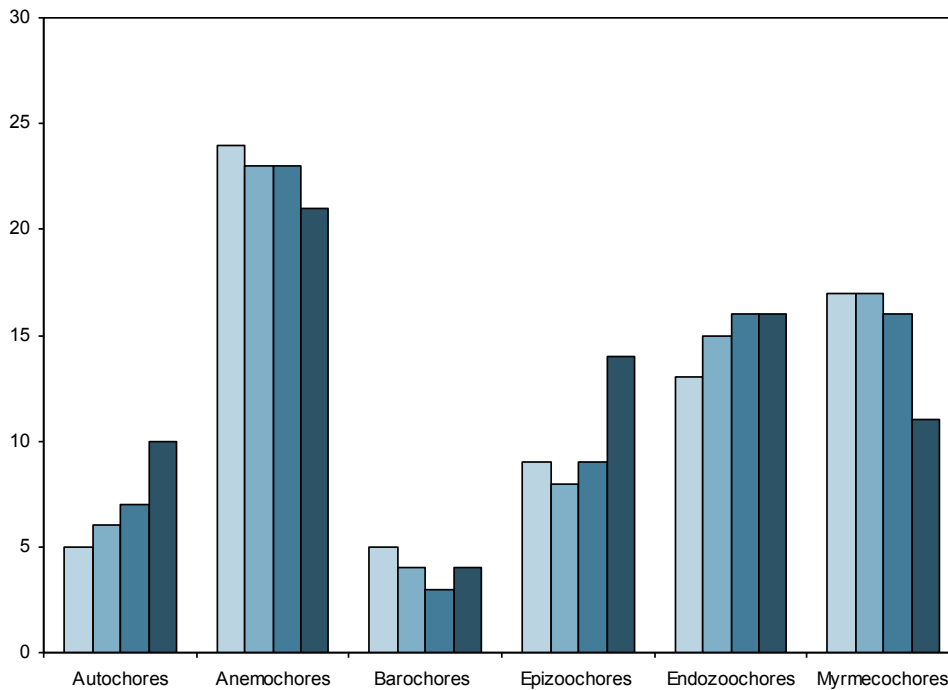
Fig. 1   Mean participation (%) of number of herb layer species of various seed dispersal modes in the studied woodlands: bright grey – ancient woodlands; bright battleship blue – woodlands aged 123–216; battleship blue – woodlands aged 71–122; dark battleship blue – woodlands aged below 71 years (seed dispersal types of insignificant participation were omitted).

(An), *Epipactis helleborine* (An), *Galanthus nivalis* (M), *Monotropa hypopitys* (B), and *Melilotus melissophyllum* (B), do not rank among rapidly dispersing plants. This list lacks epizoochores and endozoochores, except *Arum alpinum*, which occurs merely in selected sites.

The number of autochores depends predominantly on the shape and age of woodland (Tab. 3). These two factors explain as much as 98% of variation in the number of the discussed species in the studied woods. The age of woodland also significantly determines the abundance of such common woodland autochores as *Geranium robertianum* and *Oxalis acetosella*. The latter species can be found chiefly in flat-surfaced woodlands (hilltop parts of the studied area), which is evident from a significant negative dependence on the exposure index. An example of a frequently occurring autochorous woodland species that shows a distribution related mainly to the presence of rocks and landform complexity is *Lathyrus vernus*. A highly significant link between the number of autochores in the ONP and shape index may imply that the long perimeter of woodland relative to its surface area facilitates the migration of these species. The demonstrated dependence of the number of epizoochores on shape index may indicate a more frequent penetration of long-shaped woodlands by large animals that transport seeds of these species.

The number of anemochores is primarily related to the age of woodland and the presence of rocks (Tab. 3). Examples of common anemochorous woodland species with their distribution and abundance dependent significantly on woodland age include: *Milium effusum*, *Mycelis muralis*, and *Poa nemoralis* (Tab. 4). All of them are categorized as light anemochores. A large portion of species producing wind-borne seeds, particularly hovering anemochores, are epilithic species, hence the connection between the number of these species and the presence of rocks. *Senecio nemorensis* exemplifies a frequently found woodland species with distribution and abundance significantly dependent on contact with older woodland. The proximity of older woodland is an important factor particularly in the case of heavy anemochores.

The number of barochores significantly increases in older forests and forests containing rocks, as well as those bordering moist habitats (Tab. 3). This is confirmed by the results obtained from the analysis of the common barochorous woodland species *Aegopodium podagraria* (Tab. 4).

Tab. 3 Results of multiple regression analysis for species number of various seed dispersal modes.

	Minimum–maximum number of species	Age of forest	Shape index	Maximum slope inclination	Exposure	Presence of rocks	Age of the oldest adjacent forest	Contact with moist habitats	Contact with meadows or grasslands	Contact with agricultural areas	R^2 (%)
Autochores	0–5	0.05***	0.99***								98.64
Anemochores	1–24	0.27***		0.80+		0.83***					80.87
Hovering anemochores	0–9	0.09***				0.98***					96.42
Light anemochores	0–13	0.13***		0.07*		0.91***					92.63
Heavy anemochores	0–6		0.44*		0.14*		0.05**			0.41*	97.41
Barochores	0–7	0.06***				0.51***		0.47***			97.70
Epizoochores	0–10	0.09***	0.97***								94.73
Endozoochores	0–16	0.12***				0.94***					89.89
Myrmecochores	0–16	0.18***				0.85***	0.10**		0.09*		89.53
Dyszoochores	0–3	0.02***	0.69***				0.02**			0.31**	99.35

"+" – $0.1 > p > 0.05$; * $0.05 \geq p > 0.01$; ** $0.01 \geq p > 0.001$; *** $p \leq 0.001$.

The number of epizoochores is chiefly associated with the age and shape of woods (Tab. 3). The mentioned factors explain over 94% of variation in the number of epizoochores in the studied woods. The age of woods is a factor determining the distribution of frequently found epizoochorous woodland species, such as *Geum urbanum* and *Stachys sylvatica* (Tab. 4). The abundance and distribution of *G. urbanum* and *Festuca gigantea*, the latter being another common woodland species, additionally depend on contact with moist habitats.

The number of endozoochores rises with the increase in woodland age and in cases when rocks are present (Tab. 3). An example of a species that shows occurrence and abundance depends on woodland age is *Lonicera xylosteum*, and three species related to the presence of rocks are *Actaea spicata*, *Lonicera xylosteum*, and *Ribes grossularia* (Tab. 4). Some endozoochores, e.g., *Actaea spicata* and *Maianthemum bifolium*, prefer south facing or partly south-facing slopes.

Myrmecochores are quite poorly dispersing species, and therefore, their number depends significantly on the age of woodland and the contiguity of an older woodland (Tab. 3). Frequently found woodland myrmecochores whose abundance and/or distribution depend on woodland age are: *Anemone nemorosa*, *Carex sylvatica*, *Lamium maculatum*, and *Mercurialis perennis* (Tab. 4). The direct vicinity of an ancient woodlands exerts an effect on such species as: *Ajuga reptans*, *Anemone nemorosa*, *Pulmonaria obscura*, *Viola reichenbachiana*, and *Mercurialis perennis*. Neighborhood of moist habitats has an advantageous impact on the abundance of *Anemone nemorosa* and *Lamium maculatum*, and on the occurrence of *Mercurialis perennis*.

Dyszoochores (only trees and shrubs) are present in larger numbers in woodlands that have contact with older woodlands, as well as those adjacent to agricultural used land, and those having higher shape indices (Tab. 3). The above-mentioned variables explain over 99% of variation in the number of species from this group. It appears that contact with agricultural used areas is significant mainly due to its connection with the distribution of *Aesculus hippocastanum*, which may have spread from those areas where it had been planted. *Fagus sylvatica* and *Corylus avellana* are rare in young woodlands, and hence their occurrence depends on the proximity of older woods.

Tab. 4 Results of probit (Logit) and multiple regression (β coefficients) analyses for woodland species that were recorded on at least 40 studied woodland patches.

Species			Age of woodland	Area	Forest perimeter	Shape index	Mean slope inclination	Maximum slope inclination	Microrelief complexity	Exposure	Presence of rocks	Age of the oldest adjacent forest	Contact with moist habitats	Contact with meadows or grasslands	R^2 (%)
Actaea spicata	En	Logit								19.35**				8.26**	
		β													10.62
Aegopodium podagraria	B	Logit	11.7***								0.32***			12.9***	
		β					0.2*						0.19*	0.27***	19.18
Ajuga reptans	M	Logit										7.2**			
		β						0.78*							8.97
Anemone nemorosa	M	Logit	11.8***									0.22**			
		β					−0.75*					0.19*	0.25**		12.76
Carex sylvatica	M	Logit			6.51*						9.97**				
		β	0.31***										−0.25**		9.93
Dryopteris filix-mas	An	Logit					9.65**								
		β					0.29***								8.20
Festuca gigantea	Ep	Logit											7.64*		
		β											−0.17*		3.09
Galeobdolon luteum	M	Logit									22.4***				
		β									0.45***				21.02
Geranium robertianum	Au	Logit	14.4***												
		β	0.36***												13.64
Geum urbanum	Ep	Logit	9.75**											4.01*	
		β					−0.73*	0.88**					0.20*		11.90

Tab. 4 Continued

Species			Age of woodland	Area	Forest perimeter	Shape index	Mean slope inclination	Maximum slope inclination	Micro-relief complexity	Exposure	Presence of rocks	Age of the oldest adjacent forest	Contact with moist habitats	Contact with meadows or grasslands	R^2 (%)
Lamium maculatum	M	Logit	13.1***												16.00
		β	0.28***												
Lathyrus vernus	Au	Logit							16.8***		15.1***				22.02
		β									0.47***		0.20*		
Lonicera xylosteum	En	Logit	5.73**								9.98**				24.50
		β	0.30***								0.25**				
Maianthemum bifolium	En	Logit			15.37**					11.99*		7.07**			12.68
		β			0.34***							−0.16*		−0.18*	
Mercurialis perennis	M	Logit	11.9***	7.02**		6.66**				12.12*		4.72**	11.36**		29.27
		β	0.49***	−0.15*											
Milium effusum	An	Logit	6.88**		5.59*		6.45*								5.95
		β	−0.24**												
Mycelis muralis	An	Logit	8.34**												21.20
		β	0.25**					0.27**							
Oxalis acetosella	Au	Logit													3.91
		β	0.2*							−0.2*					
Poa nemoralis	An	Logit	8.33*												10.23
		β								0.19*			0.21*		
Pulmonaria obscura	M	Logit									13.0***				15.59
		β									0.22*	0.20*		0.17*	

Tab. 4 Continued

Species		Age of woodland	Area	Forest perimeter	Shape index	Mean slope inclination	Maximum slope inclination	Micro-relief complexity	Exposure	Presence of rocks	Age of the oldest adjacent forest	Contact with moist habitats	Contact with meadows or grasslands	R^2 (%)
Ribes grossularia	En	Logit			4.71*					8.96**				
	β									0.30**			0.2*	13.11
Senecio nemorensis	An	Logit									5.92*	6.95*		
	β							0.18*			0.19*	−0.21*		9.88
Sorbus accuparia	En	Logit												
	β							0.17*						3.02
Stachys sylvatica	Ep	Logit	22.4***											
	β**	0.37*									15.6***			14.13
Viola reichenbachiana	M	Logit												
	β										0.30***			10.09

"+" – 0.1 > *p* > 0.05; * 0.05 ≥ *p* > 0.01; ** 0.01 ≥ *p* > 0.001; *** *p* ≤ 0.001.

Discussion

Studies by various authors indicate a positive dependence between the species richness and age of woodlands, showing ancient woodlands as sources of diaspores and centers of diversity [2,7,9,14,45].

All groups of woodland species representing different seed dispersal types showed a connection to woodland age. The strength of this relationship is not always inversely proportional to migration rate. This proves an impact from factors other than migration rate on the colonization of forest communities. Many authors also point out the importance of habitat conditions in the effective colonization process of recent woodlands (e.g., [9,46,47], cf. [48]). The principal factor that determines diaspore germination is soil moisture. Low moisture of the litter layer and soil do not usually facilitate woodland species growth, hence preventing the colonization of such sites by these plants [12]. Soil type, composition and reaction have been shown to affect species distribution patterns in woodlands [9,46,49,50]. It is regarded that soil type may facilitate or hinder forest regeneration. For example, moist brown earths favor colonization by woodland species and the regeneration of forest communities [10]. Dry calcareous soils, in turn, are rather unfavorable to the dissemination of woodland plants. Such soils, covered by a poorly degrading litter layer, may cause a several times lower species migration rate relative to the colonization rate in forests growing on moist brown earths [46]. It has been observed that a thicker litter layer substantially slows down the process of woodland colonization. It has been shown that coniferous litter impedes the germination and development of woodland species to a larger extent than deciduous litter. This is caused by its slower decomposition and acidification of soil [9,51]. Rapidly decomposing litter, which provides a thick layer of humus, correlates positively to the occurrence of woodland species [51]. It has also been discovered that the growth of grasses and other hemicryptophytes is more strongly inhibited by a thick litter layer than that of spring geophytes. It is difficult

for such species as *Holcus mollis*, *Poa trivialis*, *Poa nemoralis*, and *Viola riviniana* to grow through the litter layer, in contrast to individuals of *Anemone nemorosa*, *Actaea spicata*, *Convallaria majalis*, and *Lathyrus vernus*, which easily penetrate the layer with their sprouts [9,52]. Secondary woodlands growing in post-agricultural areas are marked by much more fertile soils. They show higher phosphate and nitrate levels, and a higher pH, even 100–200 years after the formation of woodland. This facilitates the retention of field or meadow species and strongly decelerates the process of these areas being colonized by woodland plants [13,24,53–55]. However, some woodland species tolerate high nutrient levels and can therefore fairly quickly colonize such areas, forming numerous populations, e.g., *Stachys sylvatica*, *Circaea lutetiana*, *Geum urbanum*, *Glechoma hederacea*, *Ficaria verna*, *Adoxa moschatellina*, and *Ajuga reptans* [56]. Other research indicates that ancient woodlands may also have higher nitrogen content than secondary woodlands [57]. In the ONP, a major role has been played by historical factors and forest management, including numerous plantings of coniferous trees in the hilltop part in the first half of the twentieth century, which affected the litter composition and might have caused soil acidification, and the proximity of fields, from which fertilizers permeate and also affect soil pH and composition. Another important circumstance is the fact that most ancient woodlands in the ONP – sources of forest species diaspores – lie in valleys. Such a location does not facilitate the colonization of higher sites.

The participations of species with different seed dispersal mechanisms in woodlands of different ages in the OPN are illustrated by the impact of the dispersal rate on colonization processes. According to the findings of various authors, zoochores are the best colonizers (fastest and spreading over largest distances), endozoochores first, followed by epizoochores; anemochores are slightly poorer, with autochores, myrmecochores, and barochores closing the list as the poorest colonizers [7,12]. Distances covered by diaspores of anemochorous woodland species are short compared to the species of non-woodland communities spreading in the same way; additionally, wind force and direction play a lesser role in this case, though they facilitate a higher migration rate and a more even distribution of these plants [58]. If winds blow in a particular direction, they only enhance species colonization in that direction [59].

Woodland plant seeds that travel the longest distances are those which are animal dispersed, both adhering to and eaten by animals [1,7,55,56]. The migration of zoochores may progress over very large distances across areas unsuitable for these species. However, there are differences in migration distances; species producing seeds that enter the digestive track, e.g., of migratory birds, may be transferred to distant locations. Large herbivorous animals, or even hares, can disperse plants for over 125 meters in one year [60]. On the other hand, species with seeds consumed by small forest rodents or birds that occupy small territories, can only migrate short distances [7]. It has been observed that woodlands colonization by species producing seeds (fruit) eaten by birds is affected by the pattern and vertical structure (stratification) of vegetation. Larger numbers of individuals representing these species were recorded in sites that allowed birds to perch longer, compared to other sites [61]. Because of constraints to wild animal migrations, particularly of large herbivores, and the dwindling of traditional animal husbandry, the abilities of epizoochores and endozoochores to colonize new woodland areas have been limited, especially regarding isolated areas, which causes the depletion of their diversity [7,60].

Observations made by Dzwonko and Loster [12] indicating that some species form isolated clusters in recent woodlands via vegetative propagation are in line with the findings from the Ojców forests. This applies to such species as: *Vaccinium myrtillus*, *Maianthemum bifolium*, *Polygonatum multiflorum*, *Convallaria majalis*, *Melica nutans*, and *Mercurialis perennis*. Groups of individuals belonging to these species are often isolated in secondary woodlands, given the small probability of a certain area being recolonized by individuals developing from seeds that come from distant ancient woodlands [62]. Colonization by forest plants is more rapid in newly formed woodlands if the tree canopy is denser [15,17]. The thinning of the tree stand adversely affects this process. Heavy shading hampers the penetration and development of non-woodland species, restricting their flowering and seed production, while facilitating the vegetative propagation of woodland species, such as: *Aegopodium podagraria*, *Galeobdolon luteum*, *Ficaria verna*, *Rubus hirtus*, or *Milium effusum* [10].

The results obtained are partly consistent with the classification of woodland species, according to migration rate and habitat tolerance, proposed by Verheyen and Hermy [54], based on research of secondary forest succession in Belgium. The aforementioned authors divided them into four groups: (*i*) species in which mainly dispersal limitations and habitat conditions determine migration to new areas, e.g., *Primula elatior*, *Arum maculatum*, *Galeobdolon luteum*; their occurrence in new sites weakly depends on woodland age; (*ii*) species whose migration is limited only by poor dispersal; their occurrence in new sites is related to woodland age, and chiefly to the distance from ancient woodland, e.g., *Anemone nemorosa*; they are marked by broad ecological tolerance to habitat conditions; (*iii*) species for which recruitment in new sites is independent of the distance from an ancient forest but dependent on woodland age; examples are *Paris quadrifolia* and *Polygonatum multiflorum*; their dissemination is unrestricted due to endozoochorous dispersal; (*iv*) species for which dispersal and recruitment limitations are of lesser importance; examples may be: *Aegopodium podagraria*, *Geum urbanum*, *Ficaria verna*, *Glechoma hederacea*, *Ajuga reptans*, and *Adoxa moschatellina*. According to the mentioned authors, these plants show broad ecological tolerance to various factors and spread relatively well, even if they do not have adaptations to such long-distance dispersal. For comparison, the most commonly found species in the ONP with dispersal strongly dependent on the proximity of an ancient woodland are: *Ajuga reptans*, *Anemone nemorosa*, *Asarum europaeum*, *Maianthemum bifolium*, *Mercurialis perennis*, and *Senecio nemorensis*, and those with occurrence dependent also on the age of a secondary woodland are: *Anemone nemorosa*, *Carex sylvatica*, *Cephalanthera longifolia*, *Hepatica nobilis*, *Lonicera xylosteum*, *Geranium robertianum*, *Geum urbanum*, *Lamium maculatum*, *Mercurialis perennis*, *Milium effusum*, *Mycelis muralis*, *Poa nemoralis*, and *Stachys sylvatica*.

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