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The negative impact of intentionally introduced *Quercus rubra* L. on a forest community

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Abstract

Some alien woody species used in commercial forestry become invasive and, as invaders, cause major problems in natural and semi-natural ecosystems. However, the deliberate introduction of aliens can bring unintended negative changes also within areas of their cultivation. This paper presents the effects of the intentional introduction of the North-American *Quercus rubra* in European mixed Scots pine-Pedunculate oak forests (POFs): *Querco roboris-Pinetum* (W. Mat. 1981) J. Mat. 1988. Phytosociological data from field research combined with GIS data analysis of the current distribution of Northern Red oak in the studied habitat were used to determine the composition and structure of forest communities in plots with and without *Q. rubra* participation.

The results show that *Q. rubra* significantly reduces native species richness and abundance, both in old-growth and in secondary (post-agricultural) forests. Not one resident vascular plant benefits from the introduction of Northern Red oak and only a few are able to tolerate its co-occurrence. The natural restocking of all native woody species is also strongly limited by this alien tree.

The introduction of Northern Red oak significantly limits the environmental functions of the POF ecosystem and weakens its economic and social aspects. However, its further cultivation is justified from an economic point of view, as the essential function of the studied forests is commercial timber production, and the introduction of this fast growing alien tree supports the provisioning ecosystem services. A clear description of the level of trade-off between the accepted negative and positive effects of the introduction of *Q. rubra* on forest ecosystem services requires further interdisciplinary studies.

Keywords: Northern Red oak; biodiversity; commercial forestry; old-growth and secondary forests; ecosystem services

Introduction

A substantial part of contemporary commercial forestry is based on the cultivation of intentionally introduced non-native woody species [1–3]. This approach is justified by the numerous positive silvicultural properties of the planted trees, such as their fast growth and the wide range of applications of their wood products, as well as the high capability of aliens to adapt to a wide variety of environmental conditions, their easy establishment and their high resistance to negative biotic and abiotic impacts in new areas of introduction. Unfortunately, the same species characteristics, which are valuable for forestry, generate serious problems when the alien becomes invasive [4–10]. Introduced species that spread from plantations to natural and semi-natural areas have a considerable impact on the properties and functions of the ecosystem and cause ecological, economical and social damage [11–13]. However, alien trees planted as monocultures or deliberately introduced as a "biocoenotic admixture" for enrichment of impoverished forest stands can also bring unintended negative changes within the areas of cultivation [14–16]. Invading woody species alter natural regeneration regimes by the utilization of various mechanisms to dominate understory environments and outcompete native species for available resources [17–20]. Self-sown young individuals of planted exotics occupy the niches of autochthonous plants and inhibit both their recruitment and growth [21–24]. An understanding of the positive and negative effects of the introduction of alien species on native ecosystems is fundamental to sustainable management and to proper nature conservation policy [25–28]. It is also an essential part of assessing of the influence of the alien species on ecosystem services [29,30], especially in forests which are altered, disrupted or degraded by commercially-important but invasive plants introduced deliberately [21,31–33].

In this paper, we analyze the effects of Northern Red oak *Quercus rubra* L. introduction on European mixed pine-oak forests. It is one of 582 North American woody species

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brought to Europe before 1915 [34] and was first intentionally introduced as an ornamental in the XVII century [35,36]. Two hundred years after its successful introduction in forest ecosystems at the end of XVIII century [37], it has become one of the most common and commercially-important broadleaved woody species of alien origin [38,39]. At present, *Q. rubra* is widespread in European forests [40], including Polish ones (the Information System of the National Forest Holding State Forest – SILP), and in the majority of territories it is noted as "established" (Fig. 1).

Quercus rubra is planted in a wide range of forest habitats suitable for deciduous as well as for coniferous trees [36,41]. Foresters describe it as the "wonder plant" (sensu Richardson [4]) due to its numerous positive characteristics [38,42,43], and in the timber industry it is called an "American Beauty" [44]. However, the positive perception of *Q. rubra* is challenged by some studies, which report that it has negative effects on forest biodiversity [45–48]. The inclusion of Northern Red oak to the official list of invasive alien species in the Czech Republic [49], and its description as "invasive" in Poland [50,51] and in Lithuania [52] is noted by the supporters of *Q. rubra* introduction as an unjustified misinterpretation of the facts [53].

In Poland, the misunderstandings between supporters and opponents of further *Q. rubra* cultivation are based on a lack of empirical data concerning the positive and negative ecological, economical and social effects of *Q. rubra* introduction, and by the ambiguity of general rules on non-native species use. Current Polish legislation limits the introduction of alien plants [54], although a number of exceptions exist for species which are used in rational forestry and in agriculture, or are planted in urban, park and garden areas as ornamentals [55]. Similarly, the rules and standards of sustainable forest management from 2003 also banned the introduction of alien trees in Polish forests and even suggested the gradual elimination of some of those already introduced (like *Padus serotina*), but these rules did not concern exotics used in plantations for timber production [56]. Furthermore, the increasing pressure of conservationists who oppose any introduction of alien trees, even in plantations, is regarded as a limitation on forest management and a waste of long-standing and fruitful studies on the acclimatization of non-native woody species useful in commercial forestry. Consequently, as the new regulations concerning forest cultivation [57] do not mention the problem of alien species at all, this issue has reached an impasse.

Even though *Q. rubra* is reported to be invasive [50,51], it was not included in the newest list of alien plants which may be a threat to native species or natural habitats [58], which justifies its further introduction as a timber tree, and the danger of its invasion is not regarded as being serious [53]. The solution to this conflict requires an understanding of both the real and potential, positive and negative, ecological and economical effects of the introduction of *Q. rubra* to forest ecosystems [59].

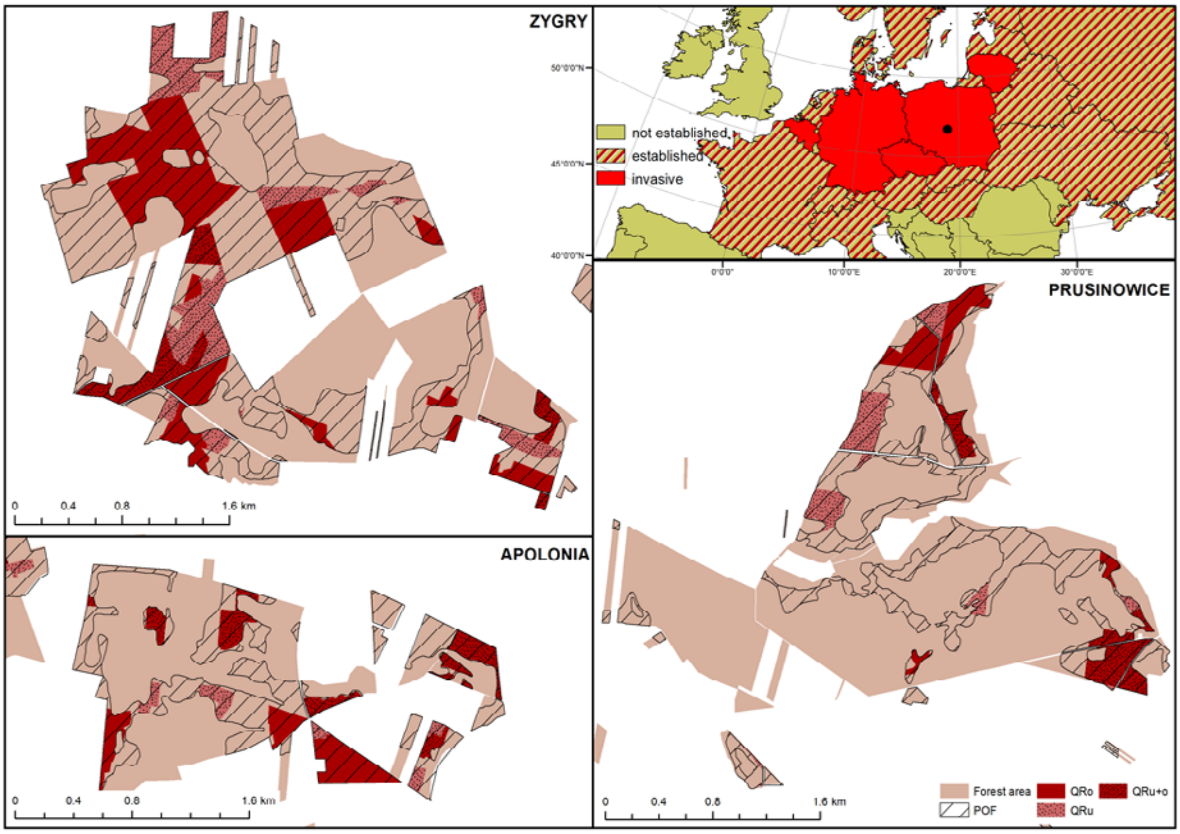

Fig. 1 Location of the study area on the map of *Quercus rubra* distribution in Europe, and the distribution of this alien tree within a mixed Scots pine-Pedunculate oak forest (POF) habitat in three forest complexes in the Poddębice Forest District (central Poland), where Northern Red oak was introduced, and at present it occurs in the overstory (QRo), in the understory (QRu) or in both layers (QRu+o) of the POF (data source: the distribution and statue of *Q. rubra* in European countries is based on NOBANIS data and additionally on Redei et al. [39] Riepšas and Straigytė [52], Verloove [101], and Medvecká et al. [102]. GIS maps were obtained using SILP data from 2011.

This paper addresses five main points: (***i***) how the native plant community is affected by Northern Red oak; (***ii***) how different abundances of *Q. rubra* affect structure and species composition, and whether there are any susceptible/resistant species to this alien species; (***iii***) whether *Q. rubra* influences native sapling growth; and, (***iv***) whether the negative/positive impact of *Q. rubra* on biodiversity depends on site history (old-growth forests versus secondary forests).

Material and methods

Study area

The studies were conducted in forest complexes in the Poddębice Forest District located in the central part of Poland (Fig. 1). The old-growth forests (forests with continuous sequence of tree generations) and secondary forests growing on former agricultural land (ancient and recent forest complexes sensu Peterken [60]) are spread across landscape dominated by agricultural fields [61]. The total woodland area amounts 17.5 thousand ha, constituting 21.1% of the forest district area, in which 4.7 thousand ha of habitat is suitable for Scots pine-Pedunculate oak forest (POF) occurrence. The sites are characterized by well-drained but moist mineral soils, usually sandy loams, which are acidic (pH ~5.0), with low nutrient availability (SILP data).

The POF forests are found between conifer and broad-leaved forests and the habitat is naturally occupied by *Querco roboris-Pinetum* (W. Mat. 1981) J. Mat. 1988 community [62]. The two- or three-layered overstory comprises *Pinus sylvestris* and *Quercus robur* with an admixture of *Betula pendula*, *Populus tremula* and rare examples of *Carpinus betulus*. *Frangula alnus*, *Sorbus aucuparia* and *Juniperus communis* are common subcanopy associates. The herb and moss layers are built from numerous acidophilous, oligo- or mezotrophic species, "spreading" both from conifer and from broad-leaved forest habitats [63]. Species characteristic of coniferous forests – *Vaccinium myrtillus*, *V. vitis-idaea* and *Trientalis europaea*, which prefer semi-light or sunny sites, dominate in the herb layer. *Maianthemum bifolium*, *Melampyrum pratense*, *Luzula pilosa*, *Pteridium aquilinum* and *Calluna vulgaris* are also frequently noted. The species preferring semi-shadow and shadow sites, connected to deciduous forests are numerous, but they usually achieve low abundance. However, the occurrence of *Polygonatum odoratum*, *Peucedanum oreoselinum*, *Viola riviniana*, *Solidago virgaurea*, *Scorzonera humilis*, *Veronica officinalis*, *V. chamaedris*, *Convallaria majalis* and *Fragaria vesca* distinguishes POF communities [62,63].

The studied forests were planted as timber forests, and Scots pine, admittedly suitable to the POF habitat, is much more common here than in natural assemblages. Moreover, in around one fifth of the POF area, the native oak species *Q. robur* has been supplanted by the Northern Red oak [41]. The intentional introduction of this alien tree started at the beginning of the XX century: the oldest *Q. rubra* individuals are 104 years old (SILP data). In the majority of forest patches, *Q. rubra* was introduced as a "biocoenotic admixture", where it was planted in numerous small clusters, 10 × 10 m in area, or as single individuals regularly dispersed within Scots pine stands growing on both in old-growth and in secondary forests, where it has become the second timber tree. At present, forests where *Q. rubra* dominates in the tree stand layer constitute 292.6 ha of the POF (SILP data). This tree occurs both in the overstory (introduced) and in the shrub layer (introduced and/or self-sown) for another 259.9 ha. A further 266.1 ha of the POF contain the plots with *Q. rubra* planted in last 20 years, and where it is noted only in the shrub layer. The 332 isolated patches with introduced *Q. rubra* are widely dispersed within the area of the POF habitat: three examples are presented in Fig. 1. The majority of introduced trees, representing 67% of the introduction area, have already achieved reproductive age.

Data collection

The effects of the introduction of *Q. rubra* to the POF were researched in 2012: this was preceded by an analysis of SILP data on POF habitat distribution, carried out in GIS (ArcGIS 10.0), and on *Q. rubra* occurrence. Field sampling was conducted using phytosociological reléves, sample plots, located in homogenous patches of vegetation, far from the forest edge to avoid border effects, either with introduced *Q. rubra* (QR plots) or without QR (reference plots). The 83 sample plots, including 18 reference ones, were taken within mature timber plantations older than 60 years. In each plot, the cover of all vascular plant species (herbs, shrubs and trees) was estimated using a six-degree cover-abundance scale from "+", representing a few individuals covering less than 1%, to "5", representing plant species covering more than 75% of the plot area [64], which allowed an estimation of both the number of species and the proportion of the area covered by them. Additionally, the number of *Q. rubra* individuals with tree trunk perimeters greater than 10 cm was counted for each sample plot.

Data analyses

For each sample plot, six floristic indices, which characterized the diversity and the condition of forest communities, were counted. The richness of the plant species within the sets of plots with *Q. rubra* and without *Q. rubra* was described by the mean number of species (*Ns*) per sample plot. The species diversity in QR plots and in reference plots was characterized by the Shannon diversity index: $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion of the ith species frequency of the sum of all species frequencies and by the evenness index (J'). The Shannon index and evenness were calculated by MVSP software (version 3.13, Kovach Computing Services). Before this analysis, original species cover values were transformed to mean percentages of species cover (+ = 1.0; 1 = 5.0; 2 = 17.5; 3 = 37.5; 4 = 62.5; 5 = 87.5). For trees and shrubs the cover index was calculated as a sum of percentages cover from each layers in sample plot where the species was noted. We assumed that the cover index for species in sample plot cannot be higher than 100. The differences in abundance of species in QR plots and reference one are described by the sum of percentage cover (*Sci*).

The naturalness of plant community in plots was characterized by the number of species characteristic to a POF phytosociological unit (*NCs*) and by their sum of percentage cover (*SCci*). Species characteristic to POF were categorized according to Matuszkiewicz [63].

Next, the statistical differences between plots with and without *Q. rubra* were analyzed with the Student's *t*-test ($P < 0.05$). The normality was checked with the Shapiro–Wilk test, and homogeneity of variance with Levene's test. Due to the lack of normal distribution of the calculated indexes, a Box–Cox transformation was used. The linear relationship between the number of *Q. rubra* individuals and the value of floristic indices (*H'*, *J'*, *Ns*, *NCs*, *Sci*, *SCci*) was also examined. Pearson's correlation coefficient with its significance (*P* value <0.05) was also calculated, also after Box–Cox transformation. All these statistical analyses were performed using the STATISTICA package (version 10.0, StatSoft Inc., Tulsa). DCA and CCA in the CANOCO program version 4.5 [65] were used to characterize the general pattern of variation of sample composition and species distribution.

In two canonical analyses, the number of *Q. rubra* individuals and the sum of percentages cover of *Q. rubra* from a different cover layer were used as supplemented data. The percentages of species cover were used in canonical analysis: species whose frequencies were lower than 10% were excluded from the analysis.

On the basis of these results, the species resistant (winners) and sensitive (losers) to *Q. rubra* occurrence were indicated. It was assumed that the changes in POF herb layer composition were likely caused by the changes in light condition under the *Q. rubra* canopy [66], which is much closer than in natural POF forests, so the preferences of "winners" and "losers" to the light condition were characterized using Ellenberg's indicator values (*EIV*) [67].

Results

Research carried out in the POFs showed that the occurrence of introduced *Q. rubra* is an important factor leading to changes in the composition of native flora. DCA analysis shows that the sample plots with *Q. rubra* create a separate set of patches, which are displaced relative to the references in the plane of the first ordination axis. The first axis accounts for 70.2% of variance and the second only 4.7% in the data set. The direction of the shifts of the infected area against the reference is consistent with the direction of the vector describing the number of *Q. rubra* individuals and sum *Q. rubra* cover index (Fig. 2).

Impact of *Q. rubra* occurrence on POF biodiversity

The obtained results indicate that *Q. rubra* reduces POF diversity. Its occurrence in the studied forest plots resulted in a statistically significant reduction of biodiversity, the Shannon index (*H'*), total number of species (*Ns*) and number of species characteristic of coniferous forest (*NCs*; Student's *t*-test, $P < 0.005$). QR plots were characterized by a lower sum of all species cover index (*Sci*). No significant differences were found in the evenness index (*J*), the value of which was not dependent on the presence of *Q. rubra* (Tab. 1).

A strong linear relationship was found between the number of individual *Q. rubra* and the value of the parameters describing biodiversity (Fig. 3). The Pearson correlation index (*r*) reached a value between −0.48 to −0.64, confirming that biodiversity dramatically decreases as the number of

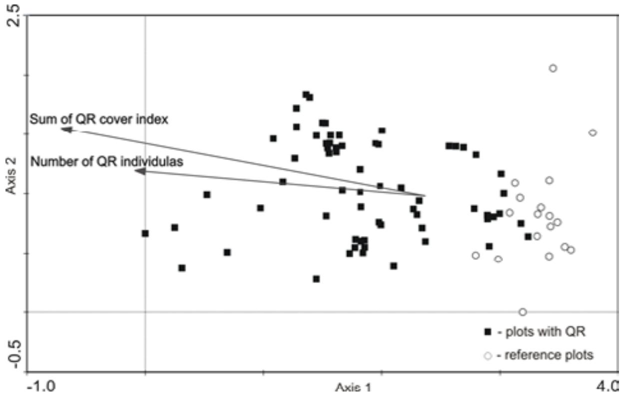

Fig. 2 Distribution of individual samples in the ordination diagram for the first two axes of the DCA with passively projected explanatory variables (number of QR individuals, sum of QR cover index).

Q. rubra individuals increase ($P < 0.005$). Among all analyzed diversity indicators, the Shannon index (*H'*) demonstrated the largest decline.

Indicator values: 'winners' and 'losers'

The total number of herbaceous plants noted in studied POF plots amounted to 38. The QR plots contained 27 species and the reference plots – 29. The results show that no herbaceous species would have a significantly higher average coverage index in the *Q. rubra* plots in comparison to the reference plots. Only one species, *Dryopteris carthusiana*, has a slightly higher frequency and mean cover index in communities with the introduced alien. *Polygonatum odoratum*, *Luzula pilosa*, *Vaccinium vitis-idaea*, *Trientalis europaea*, *Festuca ovina* and *Convallaria majalis* are relatively well able to tolerate *Q. rubra* occurrence (Fig. 4). These species grow in a wide range of habitats and they are commonly noted in mixed coniferous as well as in mixed deciduous forests. Six species: *Vaccinium myrtillus*, *Calluna vulgaris*, *Pteridium aquilinum*, *Melampyrum pratense*, *Carex pilulifera* and *Anthoxanthum odoratum* are indicated as very sensitive to *Q. rubra* introduction (Fig. 4). This group includes species more strongly associated with coniferous and mixed coniferous forests. The species sensitive to *Q. rubra* occurrence prefer semi-light or sunny sites and their mean light *EIV* amounts to 5.1, while the species more resistant to *Q. rubra* tolerate shade and semi-shade sites – their mean light *EIV* amounts to 3.8.

The QR plots were rarely settled by *Padus serotina*, another alien North-American species in Polish forests [50], however, its saplings were noted equally often in reference plots.

Impact of QR occurrence on natural restoration of native trees

Plots with *Q. rubra* are distinguished from the reference plots by their significantly lower mean cover index of saplings in the shrub layer and seedlings in the herb layer (Fig. 5) of native trees. The only species which *Q. rubra* introduction has little influence on is *Sorbus aucuparia*. All remaining native woody species fail to compete successfully with *Q. rubra* (Fig. 4).

Tab. 1 Differences in Shannon index, evenness, number of species, number of coniferous forest species and sum of cover index in invaded plots and reference plots.

Biodiversity indices	Average for QR plots	Average for references plots	*t* statistic	*P* value
Shannon index (*H'*)	1.45 ±0.33	1.71 ±0.22	−3.23	<0.005
Evenness (*J*)	0.63 ±0.09	0.61 ±0.07	0.90	ns
Number of species (*Ns*)	7.03 ±3.15	14.72 ±1.58	−8.19	<0.001
Sum of all species cover index (*Sci*)	118.40 ±79.13	261.50 ±59.61	−6.68	<0.001
Number of coniferous forest species (*NCs*)	1.63 ±1.31	3.39 ±1.25	−4.75	<0.001
Sum of coniferous forest species cover index (*SCci*)	23.36 ±36.27	72.39 ±31.45	−5.64	<0.001

The significant of differences was tested by Student's *t*-test ($P < 0.05$) after Box–Cox transformation.

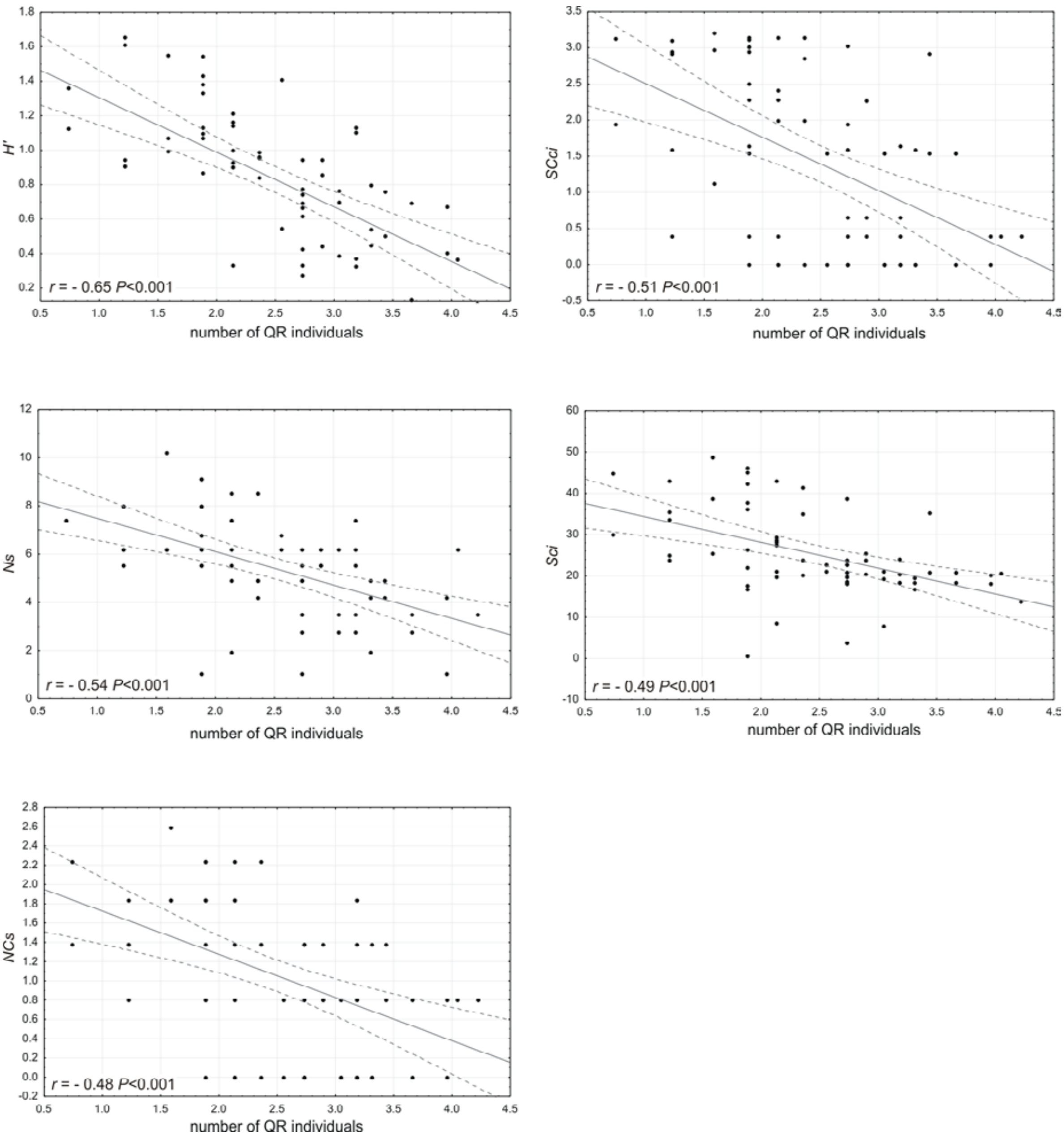

Fig. 3 Linear correlations between number of QR individuals and Shannon index (*H'*), number of species (*Ns*), number of species characteristic to coniferous forests (*NCs*), sum of all species cover index (*Sci*) and sum of cover index of species characteristic to coniferous forests (*SCci*); *r* = Pearson correlation coefficient ($P < 0.001$). All data before analysis were normalized by Box–Cox transformations.

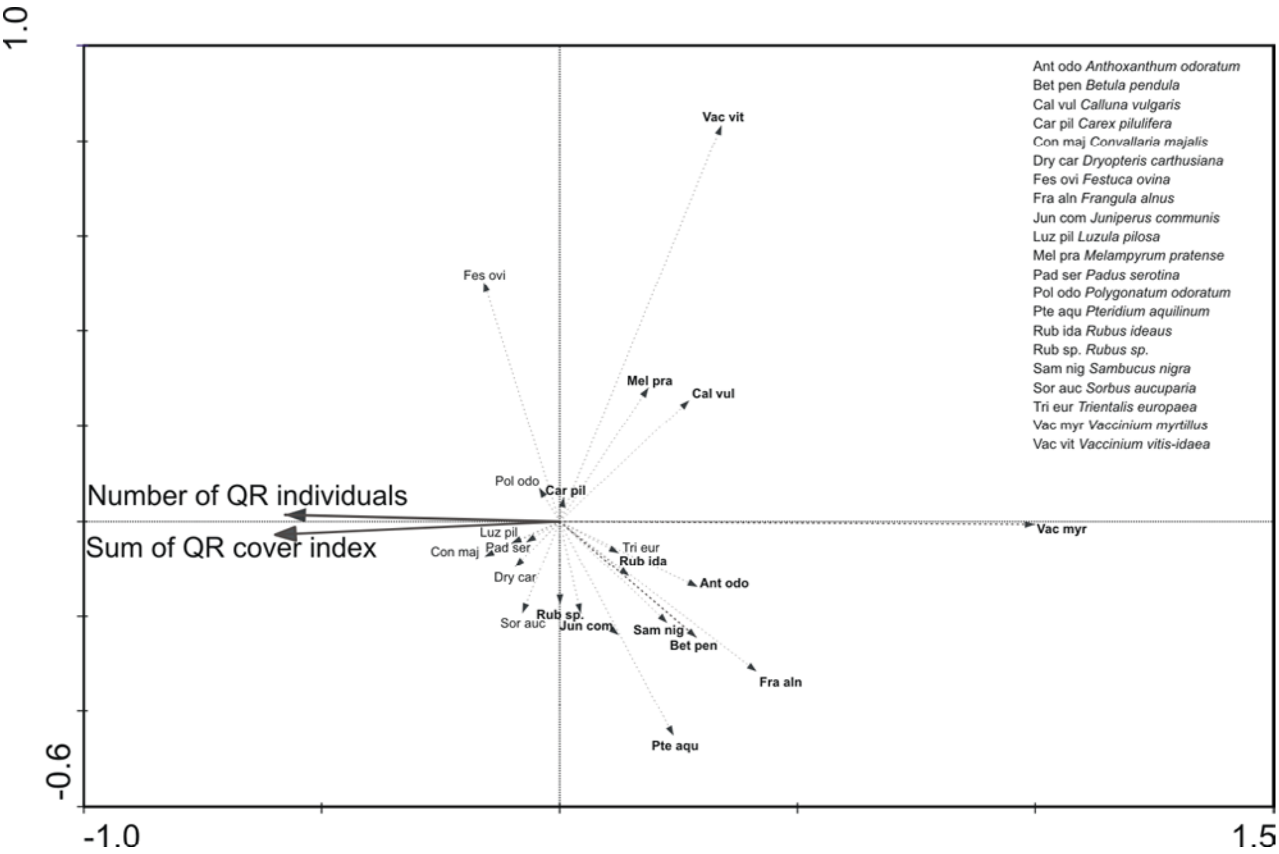

Fig. 4 Distribution of selected plant species in the ordination diagram of CCA for the first two axes with passively projected explanatory variables (number of QR individuals, sum of QR cover index). Eigenvalues were 0.75 for the first axis and 0.07 for the second in the biotic CCA. Species in bold have a significantly lower cover in QR plots (Student's *t*-test, $P < 0.05$).

Effect of *Q. rubra* introduction on forest communities located in old-growth and in secondary forests

Plots with *Q. rubra* growing in areas permanently used as forest land were characterized by a higher average number of species characteristic of POF and by a higher mean cover index than the plots located within forests established on former agricultural lands (Fig. 6).

Discussion

Quercus rubra negatively influences vascular plant species diversity and abundance (Tab. 1 and Fig. 3) and no one native species which naturally occurs in POF benefits from its introduction (Fig. 4). The drastic changes noted in plant cover are probably caused by the decrease of understorey insolation. *Quercus rubra*, like other deciduous tree-species [68–70], gives deep shadow [66], which may lead to the reduction of understorey components, mainly species preferring semi-light and sunny sites. A higher number of *Q. rubra* individuals in a forest patch and the closer *Q. rubra* canopy is associated with a greater reduction of resident plants, regardless of whether it occurs in the shrub layer or in the overstory. A shade which is too deep, created by a close overstorey of broadleaf trees, may also negatively affect shade-tolerant species [70] and complicate the natural restocking of trees [71], including invasive species like *P. serotina* [72,73] (cf: [74,75]) The increase of broadleaf tree density in coniferous forests may also result in the withdrawal of acidophilus vascular plant species as a result of changes in soil conditions [76–78]. However, no studies presently assess the impact of QR on the soil parameters.

The forest patches dominated by intentionally introduced *Q. rubra* tend to be very homogenous and extremely poor in terms of vascular plant occurrence, which may lead to a loss of the distinctiveness of the POF community. Similar negative effects of *Q. rubra* introduction have been reported from German and Lithuanian forests [48,52,79], and, more interestingly, these effects were observed in different types of forest habitat. The introduction of alien species, which outcompete resident ones in a wide range of ecosystems, may cause the homogenization of vegetation [80–85].

Studies show that *Q. rubra* significantly reduces the occurrence and the natural restoration of all native woody species (Fig. 5). Admittedly, the majority of new generation of tree stands in the studied timber forest are artificially planted, spontaneous forest restoration is rarely used, but the abundant self-reproduction of *Q. rubra* and its ability to create numerous stump sprouts after cutting, which is common in its native range [42,86], and which has been observed in European forests [46,52] may make forest regeneration after *Q. rubra* felling significantly more difficult. The vegetative reproduction of *Q. rubra* by re-sprouting may ensure its establishment and long-term maintenance

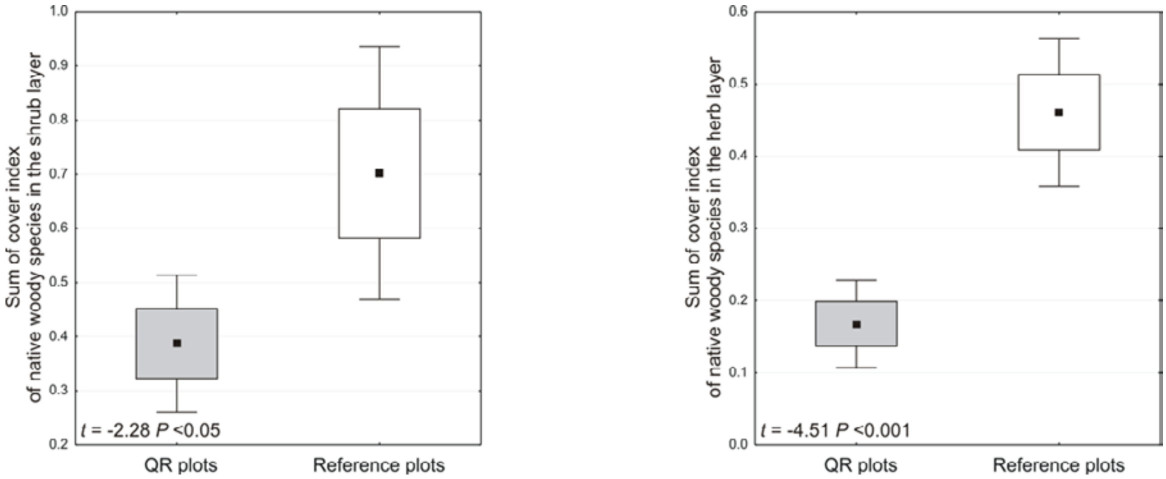

Fig. 5 Sum of native woody species cover index for QR and reference plots. The analysis was conducted separately for the shrub and herb layers. The statistical differences between plots with and without QR were analyzed with a Student's *t*-test ($P < 0.05$). All data before analysis was normalized by Box–Cox transformations.

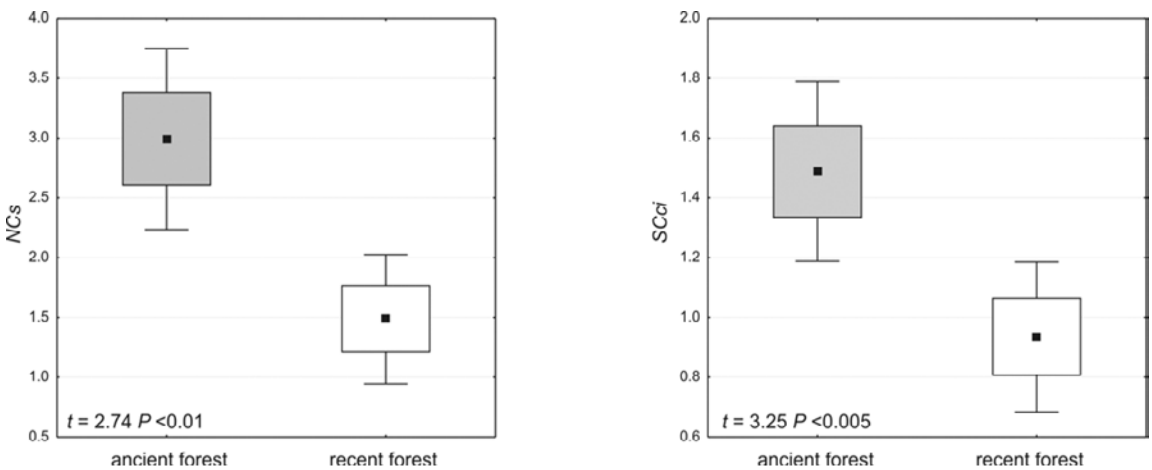

Fig. 6 The average number of coniferous forest species (*NCs*) and sum of coniferous forest species cover index (*SCci*) in ancient and recent QR plots ($df = 63$). The statistical differences between plots with and without QR were analyzed with a Student's *t*-test ($P < 0.05$). All data before analysis was normalized by Box–Cox transformations.

in the POF habitat and the increasing local reproductive pressure of this alien tree may lead to its higher invasiveness [87,88]. In a negative scenario the uncontrolled spread of *Q. rubra* limits or ultimately displaces native species in the POF ecosystem. However, the spontaneous restoration of *Q. rubra* as well as its spread outside areas of introduction, is not yet fully recognized.

Quercus rubra is still recommended as an biocoenotic admixture and is used to rehabilitate abandoned agricultural lands by afforestation [43,89]. However, the forests with introduced *Q. rubra* provide less diversified vascular understories than forests without this alien tree. QR plots located in secondary forests were not found to be richer in species number and abundance than QR plots located within old-growth forests (Fig. 6) and reference plots without the alien tree, implying that *Q. rubra* not only reduces the native forest species diversity (Tab. 2), but also it may inhibit the process of natural succession of post-agricultural plantations into natural communities. The diversification of tree species composition promoted by forest management not always favors biodiversity (for review see [71,90]), and in case of the introduction of *Q. rubra* into the studied forests, it brings a reduction in biodiversity. Although the novel ecosystems constructed by the introduced aliens are described as suitable also for resident species (e.g. Hobbs et al. [91] and Kubiak [92]), no such vascular plant species has yet been found in studied forests with *Q. rubra*.

From an economic point of view, further *Q. rubra* cultivation in the POF habitat is justified only in timber forests and only when the profits obtained from the sale of this exotic wood are higher than profits from domestic products. At present *Q. rubra* does not play an important role in the

Tab. 2 Conflicts and synergies caused by Northern Red oak introduction in mixed Scots pine–Pedunculate oak forests.

Forest ecosystem services	Impact of QR introduction
Provisioning services	
lumber, fibre and fuel wood	strong synergy
food (wild plants, mushrooms)	strong conflict
Supporting services (habitat for species & biodiversity conservation)	
vascular plant diversity	strong conflict
natural restoration of native trees	strong conflict
new habitats for native forest species (in recent forests)	strong conflict (in QR tree stands under 80 years old)
Cultural services	
aesthetic values	synergy (in Autumn)
recreation (mushrooming, hunting) and ecotourism (camping)	conflict

Ecosystem services and production functions are adapted from the Millennium Ecosystem Assessment [29] and Patterson and Coelho [32].

local timber trade. The proportion of wood obtained from *Q. rubra* cultivation in the studied area during the last decade amounted to less than 0.1% of the total acquired wood resources, while the acquisition of Scots pine wood at the same time constituted over 90% and the wood of native oaks constituted 8.4% (SILP data). In total, 92% of *Q. rubra* wood was fuel wood, 5% was used as fiber and only 3% was lumber. However, the current market value of *Q. rubra* fiber and fuel wood is equal to that of native oak wood, but the prices are higher than those of Scots pine wood [93]. Although the current profit from *Q. rubra* timber sales is low (SILP data), it can be expected to significantly increase when the stands reach logging age (100–120 years). The domestic prices of *Q. rubra* lumber are comparable to those of native oaks, and the *Q. rubra* wood is noted as precious and profitable in the timber market [53]. Furthermore, *Q. rubra* grows faster and produces more wood than European oaks [37–39], especially in post-agricultural lands [94,95].

The introduction of commercially important but invasive woody species may be accepted when the anticipated ecological, economical and social benefits exceed the costs associated with its invasiveness [96–98]. Studies show that *Q. rubra* introduction in POF definitely decreases supporting ecosystem services, however, it increases the level of provisioning services (Tab. 2).

The negative impact of *Q. rubra* on native biodiversity may be found not only in commercial forests but also in nature reserves and in nature parks where *Q. rubra* also occurs (e.g. [46,99,100]). However, the observed changes in forest structure and composition may be caused by various factors like litter quality, soil acidity and fertilization, or by different forest management options. Further studies are necessary on the mechanisms of change, on the effects of *Q. rubra* introduction, as well as on its spontaneous spread and management in the future.

Conclusions

(*i*) The introduction of *Q. rubra* causes significant changes in the structure and species composition of POF.
(*ii*) *Q. rubra* negatively influences vascular plant species diversity and abundance. No one native species benefits from *Q. rubra* introduction.
(*iii*) *Q. rubra* inhibits spontaneous restocking of POF trees.
(*iv*) Understanding the mechanisms of the changes seen in habitat conditions caused by *Q. rubra*, as well as its spontaneous spread, requires further studies.

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Authors' contributions
The following declarations about authors' contributions to the research have been made: study conception: BW, DK; field research: BW, DK; GIS and statistical analysis DK; SILP data analysis JW; analyzed the results and wrote the paper: BW, DK.

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