The invasibility of deciduous forest communities after disturbance: A case study of *Carex brizoides* and *Impatiens parviflora* invasion

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Abstract

Phytosociological records from three different woodlands, each with oak–hornbeam stands (*Tilio–Carpinetum*), were analyzed in terms of the presence/absence of two harmful species, alien *Impatiens parviflora* and native *Carex brizoides*. Records from the Białowieża Primeval Forest (northeastern Poland) represented old-growth forest, and others from the Silesian Upland (southeastern Poland) represented managed forest and invaded forest. The three sets of records were compared in terms of stand structure, Ellenberg indicator scores, and the shares of various plant functional types. Vegetation analyses also included species richness scores, Shannon–Wiener indices, and DCA and CCA ordination with the cover of the two species as variables. There were fewer differences between managed and old-growth forest than between managed and invaded forest. Invaded forest was characterized by low species richness, higher frequency of hemerophilous species, lower frequency of myrmecochores, and higher light availability and temperature. It was concluded that, of the two invasive species, *C. brizoides* is a better indicator of human-induced disturbance. Both cover and binary data explained changes in floristic composition in the presence of this species. Invasion by both species was favored by forest management practices. Their presence led to further species impoverishment, and harmed the quality of the forest floor habitat.
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Keywords: Invasions; Old-growth forest; Managed forest; Plant functional types; Phytosociological studies; Poland

1. Introduction

The impact of human activity is a major factor affecting vegetation throughout the world today. Poland lies in the zone where the natural vegetation should be broadleaved deciduous forest. Since Neolithic times, changes in vegetation cover have been accelerating. In Poland the area covered by forests has decreased to an estimated 28% of the country's territory. The majority of old-growth forests have been cleared and converted to agriculture, or altered in other ways by human activity.

The anthropogenic factors affecting forest communities vary widely. They can be divided into three groups of impacts: at the landscape level (processes connected with forest fragmentation); at the community level (effects on community structure and species composition); and at the biotope level (processes affecting habitat quality, such as soil acidification, nitrogen input or eutrophication) (Faliński, 1966, 1998; Peterken and Game, 1984; Łaska, 2001; Dzwonko and Gawronski, 2002). Alien plant invasion and the spread of expansive native species are two consequences of these changes. Nonindigenous species and indigenous plants are incorporated into plant communities, expand their range and increase their abundance, as a result of intentional (cultivation) or unintentional introduction, or inappropriate forest management practices including logging, thinning of tree stands, alteration of water regimes, removal of brushwood and litter, etc.

One of the most invasive alien species is the small balsam *Impatiens parviflora* DC, an Asiatic species very frequent in the forests of Central and Northern Europe (Pyšek et al., 1998). One of the most expansive native species is seagrass *Carex brizoides*, which is spreading due to disturbances and clearing in woodlands (Dzwonko and Gawroński, 1994; Medwecka-Kornaś, 1994; Olaczek, 1974). Both occur very abundantly in woodlands and are considered harmful. Behaviorally the two species differ completely. The former is a ballochorous annual and the latter is a perennial with a clonal growth type. Both, however, can affect the ground-layer vegetation or displace a resident community component having similar biology and

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habitat requirements. The permanent incorporation of an alien species into the structure of a previously existing or transforming community brings far-reaching changes to its dynamics and functioning (Faliński, 1998). Unmanaged old-growth forests are not usually invaded by these two species. In a comparison of forests in which the two most invasive woodland species are present and natural forests that are free of them, our study examined whether there any significant differences in the contributions of various functional plant groups, and in the community structure and habitat requirements of species in deciduous forests, and whether the differences are greater between old-growth and recent forests or between recent and invaded ones.

2. Area descriptions and methods

2.1. Study area

2.1.1. The Silesian Upland

The Silesian Upland (SU) (50°28N, 18°40E) is situated in southern Poland, covering an area of ca. 4000 km^2 (Fig. 1). It is characterized by differentiated relief and geological structure. Its central part consists of Carboniferous formations. The region is known for its deposits of important mineral resources: hard coal, zinc and lead ores, sand, gravel, dolomite, and iron ore. Mineral resource exploitation began in the early Middle Ages and intensified in the second half of the 18th century due to changes in the forms of economic activity, technical and scientific progress, and urbanization. Mean annual temperature is ca. 8 °C, and annual precipitation is 700–800 mm. The prevailing winds are from the west (SW, W, NW). The many depressions and land deformations in woodland areas there are the result of previous coal mining activity, which led to wetting or desiccation of large areas. Waste heaps, mine pits and sedimentation ponds are characteristic features of the Silesian landscape (Kozyreva et al., 2004). Woodland and scrub communities are represented by secondary deciduous and pine forests, and less often by forests of fresh, damp or wet habitats—primary oak–hornbeam forests, riparian forests or alder carrs (Kozyreva et al., 2004). The majority of primary forests were cleared and converted to arable land, wasteland, and industrialized urban areas. Some of them were afforested, mainly with coniferous species and occasionally with deciduous species (Nyrek, 1975). Some remnants of old-growth forests persisted because the habitat quality was maintained, but they have been exploited by the forestry industry.

2.1.2. Białowieża Primeval Forest

The Białowieża Primeval Forest (BPF) (52°43N, 23°50E) in northwestern Poland is the best-preserved lowland forest complex in Europe, comprising fragments of pristine nature (Fig. 1). It covers a total area of over 1500, 647 km^2 of which lies within the borders of Poland, with the remainder extending into Belarus. The climate of BPF is transitional between continental and Atlantic, making it somewhat variable (Jędrzejewska et al., 1994). Mean annual precipitation is 641 mm, while the mean annual temperature amounts to 6.8 °C. Its location on the continental watershed makes the system dependant on precipitation (Bobiec, 2002).
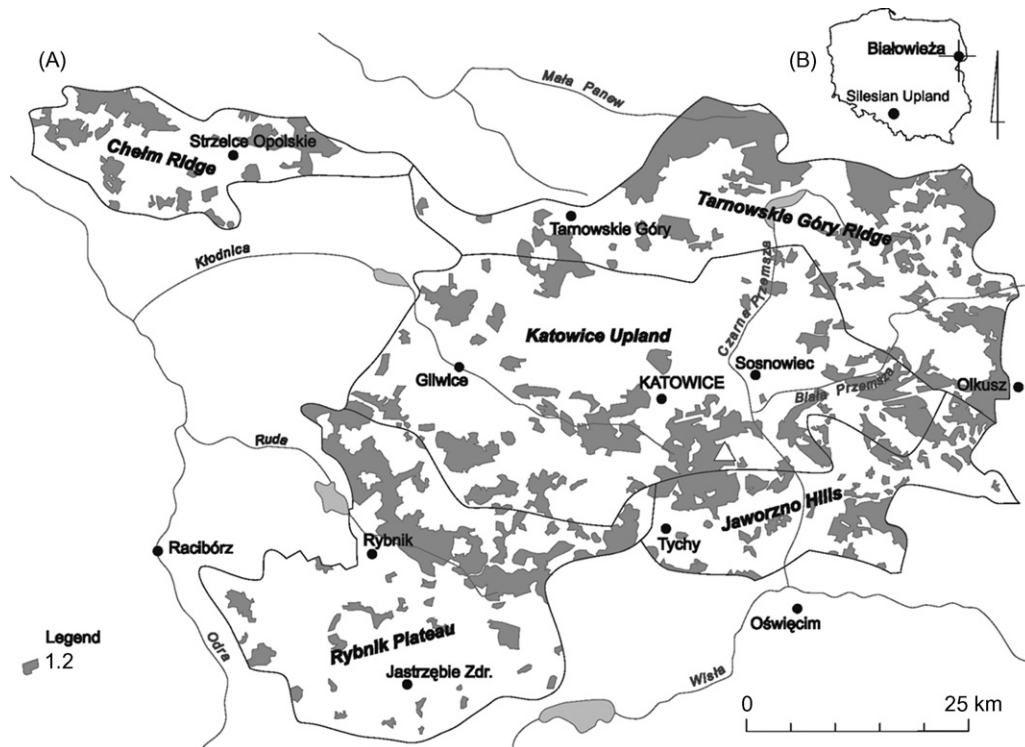

Fig. 1. Study area. Silesian Upland (A), and outline of Poland showing the locations of the Silesian Upland and Bialowieza Primeval Forest (B). 1: forests and 2: towns.
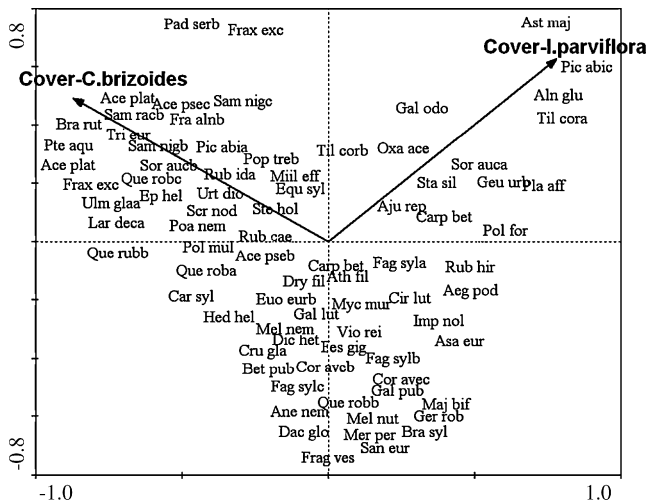
Fig. 2. Ordination diagram based on CCA in invaded oak–hornbeam forest (cover data). The arrows indicate the increasing cover-abundance of *Carex brizoides* and *Impatiens parviflora*. Species abbreviations consist of three letters of the genus and species, in the case of woody plants the fourth letter indicates the layer: a, trees; b, shrubs; c, field layer. *Acer platanoides, A. pseudoplatanus, Aeogopodium podagraria, Ajuga retans, Alnus glutinosa, Anemone nemorosa, Asarum europaeum, Astrantia major, Athyrium filix-femina, Betula pendula, Brachypodium sylvaticum, Carex sylvatica, Carpinus betulus, Circaea lutetiana, Corylus avellana, Cruciata glabra, Dactylis glomerata, Dryopteris filix-mas, Epipactis helleborine, Equisetum sylvaticum, Euonymus europea, Fagus sylvatica, Festuca gigantea, Fragaria vesca, Fraxinus excelsior, Galeopsis pubsecens, Galium odoratum, Geranium robertianum, Geum urbanum, Hedera helix, Impatiens noli-tangere, Larix decidua, Majanthemum bifolium, Melica nutans, Mercurialis perennis, Milium effusum, Oxalis acetosella, Padus serotina, Picea abies, Poa nemoralis, Polygonatum multiflorum, Populus tremula, Quercus rubra, Rubus caesius, R. hirtus, Sambucus racemosa, Sanicula europaea, Scrophularia nodosa, Sorbus aucuparia, Stachys silvatica, Tilia cordata, Trientalis europaea, Ulmus glabra, Urtica dioica, Viola reichenbachiana.*

2.2. Studied community

Over half the area of the BPF woodlands and part of the SU woodlands are oak–hornbeam forests, phytosociologically called subcontinental mixed oak–hornbeam forest (*Tilio–Carpinetum*) (Fig. 2). The oak–hornbeam woodland community consists of *Quercus robur, Carpinus betulus* and *Tilia cordata*. This association is considered to be the regional climax community in the lowlands of both SU and BPF (Matuszkiewicz, 2001). The BPF area was chosen because it represents the least disturbance of forest communities due to human activity. The oak–hornbeam forest of BPF was characterized in detail by Sokołowski (1993). *Tilio–Carpinetum* phytocoenoses of SU were chosen as examples of managed, disturbed and invaded forest. The association of this area was described phytosociologically by Cabała (1990).

2.3. Data collection

Floristic data and vegetation data were used in the present study. The floristic data were the numbers of occurrences of species in each of three sets of 40 phytosociological relevés, representing the different forest types. The vegetation data were

taken from the same sets of relevés. The first two sets were made by the authors in woodlands of SU in 1997–2002, the data of which were compiled in a table using JUICE 6.3 software (Tichý, 2002). The first group of relevés came from forest patches of oak–hornbeam community, phytosociologically identified as *Tilio cordatae–Carpinetum betuli*, with the presence of *I. parviflora* and/or *C. brizoides*. The two species were recorded occurring together in 18 of those 40 relevés. *C. brizoides* was noted in 11 relevés without *I. parviflora*, and *I. parviflora* occurred without *C. brizoides* in 10 relevés. The two species were present in 29 relevés. The second group was collected by the authors in patches of *Tilio–Carpinetum* where these two species were absent. These two groups of relevés were made at sites which other authors have identified as *Tilio–Carpinetum* (Cabała, 1990; Celiński et al., 1978; Cabała and Holeksa, 1994). The third group contained relevés made by Sokołowski (1993) in old-growth *Tilio–Carpinetum* forest in BPF. This group was treated as the reference sample.

All phytosociological relevés analyzed in this study were taken in 100 m² plots. To avoid the effect of regional differences in the species pool, only phytocoenoses of *Tilio–Carpinetum typicum* were analyzed for the whole data set. Differences in species composition were excluded and only functional species groups (guilds) were taken into consideration.

The groups of relevés were compared with respect to plant functional types, the concept of which was developed by Semenova and Van der Maarel (2000). Species were classified by life form according to Raunkiaer, given after Zarzycki et al. (2002), and by dispersal mode following the classification of Kornaś (1972) (autochore, barochore, endozoochore, epizoochore and myrmecochore). Affinities of species to a particular plant functional type are taken from several sources: Kornaś (1972), Dzwonko and Loster (2001), Frank and Klotz (1990) and Jacquemyn et al. (2001). The geographical–historical affiliations of species are taken from literature sources (Tokarska-Guzik, 2003; Zając and Zając, 1975, 1992). Definitions of apophyte, archaeophyte and neophyte follow Pyšek et al. (2004). Indices of dynamic tendencies in the number of localities and the number of individuals in them on a national scale follow Zarzycki et al. (2002). These are expressed on a four-point scale, where −2 is the most decreasing and +2 is the most increasing in range. Ecological strategies according to Grime were adopted after Frank and Klotz (1990), following Dzwonko and Loster (2001). Seven strategy types were used: competitor (C), stress tolerator (S) and ruderal (R), and four intermediate strategies indicated by the corresponding letters (CR, CS, SR, CSR). Further intermediate types were pooled as suggested by Hermy et al. (1999). Biotopic conditions were broadly characterized with average Ellenberg indicator values (Ellenberg et al., 1992) for light L, temperature T, moisture F, reaction R and nitrogen N. Computations included only binary data such as the presence/absence of species. Syntaxonomical affiliations were given after Zarzycki et al. (2002), and ancient woodland plant species indicators were distinguished following Dzwonko and Loster (2001). For better statistical treatment of the vegetation data,

the cover-abundance values of species according to the seven-degree Braun–Blanquet scale for species occurrence in phytosociological records were transformed according to the following scheme: $r = 0.1\%$, $+ = 0.5$, $1 = 5\%$, $2 = 17.5\%$, $3 = 37.5\%$, $4 = 62.5\%$, $5 = 87.5\%$ (cf. Van der Maarel, 1979). For each relevé the percentage of particular groups of species was estimated. Shannon–Wiener indices were calculated for all phytosociological records with JUICE software.

2.4. Data analysis

The significance of differences in floristic data was checked with the chi-square test. Nonparametric tests were applied to estimate differences in vegetation data between three groups of relevés; the Kruskal–Wallis test was followed by the Mann–Whitney U-test for pairwise comparisons, p-adjusted <0.017 after the Bonferroni correction (Sokal and Rohlf, 1995). Statistical analyses were done using SAS 9.1 (SAS, 2002–2003). To determine the gradients of vegetation in the presence of *C. brizoides* and/or *I. parviflora*, only the data from the Silesian Upland were used for ordination (CANOCO program; ter Braak and Šmilauer, 2002). Total changes in species composition were characterized by the length of the gradient for the first axis of Detrended Correspondence Analysis (DCA) for two types of data: cover data and binary data. Canonical Correspondence Analysis (CCA) was applied in order to examine the main directions of variation in species cover under the influence of *C. brizoides* and *I. parviflora*, which were treated as variables. The significance of the studied relationships was checked with the Monte Carlo test (499 permutations).

3. Results

3.1. Analysis of floristic data

The number of species was highest in relevés of managed oak–hornbeam forest woodlands (Table 1). In terms of the number of occurrences of species, however, the percentages of species typical for oak–hornbeam communities (i.e., of the *Carpinion* alliance, *Fagetalia* order) were highest in old-growth forest except for species of the *Querco–Fagetea* class, which were represented the most in managed forest. The share of ancient forest indicator species was highest in the woodlands of the Białowieża Primeval Forest, although it was similar to that of managed woodlands. The number of occurrences of species increasing or markedly increasing and expanding their range was highest in invaded forests; more species that are decreasing their range within Poland also occurred there, although that was not a significant relationship (Table 1).

3.2. Structure and biotopic conditions of the studied woodlands

Mean tree cover was highest in old-growth forest, and the cover of shrubs and mosses was the lowest. The lower layers had the highest cover in invaded forest, but species richness, expressed in terms of mean number of species and the Shannon–Wiener diversity index, was lowest (Table 2). Invaded woodland was characterized by the highest Ellenberg indicator values for light availability, temperature and moisture. Old-growth forest had the lowest values for light, moisture and nitrogen content indicators (Table 3).

3.3. Participation of functional groups

Generally, the greatest differences in species group shares were between invaded and old-growth forests, and the fewest were between invaded and managed forest (Table 4). Invaded forest significantly differed in endochore cover from the remaining forests: endochores were more abundant there, and myrmecochore cover was poorest. Myrmecochores were most abundant in the old-growth forest, BPF. The highest coverage of megaphanerophytes and nanophanerophytes was in invaded forest in SU; the moderate abundance of geophytes and therophytes in this type of woodland also distinguished it from the old-growth forest. Invaded forest contained the greatest abundance of species with intermediate (SR and CSR)

Table 1
Comparison of numbers of occurrences of given species groups in the relevés of the forests studied

	Invaded forest	Managed forest	Old-growth forest
Syntaxonomical affiliation			
Querco–Fagetea	239 (25) a	467 (26) b	310 (27) c
Carpinion	32 (5) a	45 (6) a	126 (8) b
Fagion	8 (1) a	28 (2) b	37 (2) b
Fagetalia	157 (29) a	284 (27) b	236 (25) ab
Vaccinio–Picetea	42 (9)	64 (8)	82 (7)
Querco robori–Pinetea	51 (8)	67 (6)	93 (7)
Dynamic tendency			
Decreasing species	18 (5)	26 (3)	47 (6)
Increasing species	224 (24) a	361 (26) b	295 (18) c
Strongly increasing species	217 (17) a	175 (10) b	185 (9) c
Old-growth forest species indicators	362 (50) a	606 (56) b	776 (59) b
Total	929 (118)	1249 (123)	1582 (119)

The numbers of species are given in parentheses. Values with the same letters do not differ significantly (Chi-square test). Rows without letters are not significant.

Table 2
Characteristics of the oak–hornbeam patches studied

	Cover of trees (%)	Cover of shrubs (%)	Cover of herbs (%)	Cover of mosses (%)	Species richness	H'
Invaded forest	71.3 a	26.4 a	87.6 a	4.5 a	21.9 a	2.17 a
Managed forest	82.0 b	20.6 a	79.0 b	1.3 b	29.1 b	2.57 b
Old-growth forest	88.9 c	4.7 b	30.8 c	0.8 a	34.4 c	2.83 c

Different letters in the column indicate significant differences at *p* level <0.017 (Kruskal–Wallis test followed by Mann–Whitney *U*-test after Bonferroni correction). H': the Shannon–Wiener index.

strategies, their cover being significantly higher there than in old-growth forest.

3.4. Interpretation of the ordination results

The CCA results show significant differentiation of species composition in the presence of sedge *C. brizoides* and small balsam *I. parviflora* in relation to presence/absence data; with respect to cover data there was significant variation only in the presence of sedge (Table 5). With *C. brizoides* there are many trees and shrubs clustered in the diagram, including the aliens (neophytes) *Quercus rubra* and *Padus serotina* (Fig. 2). Only a few herbaceous species are associated with it: *Pteridium aquilinum*, *Milium effusum*, *Trientalis europaea*, *Urtica dioica* and *Rubus* sp. Some plants typical for deciduous forest habitats are clustered with it, such as *Poa nemoralis*, *Scrophularia nodosa* and *Stellaria holostea*. Species characteristic for the class *Querco–Fagetea* (*Anemone nemorosa*, *Viola reichenbachiana*, *Melica nutans*, *Sanicula europaea*, *Brachypodium sylvaticum*, *Hedera helix*, *Impatiens noli-tangere*) are clustered at a distance from both of these invasive species. The angle between the axes of the two species studied suggests that they are indifferent in their effect on each other.

4. Discussion

4.1. Comparison of old-growth, managed and invaded forests

There is a considerable body of published data on the differences between recent and secondary forests, on the one hand, and ancient and primary forests on the other (Flinn and Vellend, 2005 and literature cited there). Most studies of a specific type of recent forest, that is, woodland characterized by the presence of a given invasive alien species, have addressed the case of invasive woody plants such as black locust *Robinia pseudoacacia* (Dzwonko and Loster, 1997) or black cherry

Prunus serotina (Godefroid et al., 2005). The differences between ancient and recent forest are a consequence not only of habitat quality but also of human pressure. Recent forests are usually managed. Abs et al. (1999) showed that primeval and managed forests (both ancient) are almost identical in terms of floristic structure. The differences basically concern their soil banks, deadwood abundance and stand structure.

Many of the known facts about old-growth forests were confirmed in this study. In terms of vegetation data, for example, our work supported the suggestion that a high proportion of myrmecochores is a good indicator of the naturalness of a woodland. They are species with poor dispersal ability and therefore almost incapable of colonizing recent forests (Peterken and Game, 1984; Grashof-Bokdam, 1997). Anemochorous species, however, were most abundant in the old-growth forest we studied, although they are usually associated with secondary communities. Endozoochores and epizoochores, quick colonizers of new sites, were most frequent in invaded and recent forests, as also shown in other work (Dzwonko, 1993). In this study the invaded forest was characterized by the lowest cover of trees and by the highest

Table 4
Comparison of the mean percentage (±S.D.) of plant functional groups in the forest communities studied

Functional group	Invaded forest (1)	Managed forest (2)	Old-growth forest (3)
Dispersal mode			
AN	38.9 ± 18.5 a	44.2 ± 15.6 a	60.2 ± 10.4 b
AU + B	18.1 ± 16.4 a	16.1 ± 9.0 a	9.0 ± 4.9 b
EN	27.3 ± 18.1 a	15.7 ± 11.0 b	10.5 ± 9.3 c
EP	5.2 ± 6.8 a	7.0 ± 9.2 a	0.5 ± 0.4 b
MY	8.2 ± 11.3 a	15.7 ± 11.4 b	17.5 ± 5.9 b
Life form			
C + Ch	2.9 ± 5.6 a	4.8 ± 6.4 b	5.4 ± 3.5 c
G	29.9 ± 17.4 a	22.4 ± 12.7 b	21.1 ± 5.6 b
M	34.5 ± 12.8 a	46.7 ± 15.2 b	63.4 ± 9.9 c
N	11.5 ± 9.7 a	7.4 ± 6.5 a	2.4 ± 2.8 b
T	7.9 ± 11.0 a	3.8 ± 6.1 a	0.6 ± 2.5 b
Life strategy			
CSR	31.3 ± 17.0 a	20.4 ± 11.6 b	25.2 ± 7.5 c
SR	7.2 ± 10.6 a	3.6 ± 6.2 b	0.1 ± 0.1 c

Means bearing the same letter are not significant at the level of 0.017 (Kruskal–Wallis test followed by Mann–Whitney *U*-test with Bonferroni correction). Only significant results are presented. *Abbreviations*: M, megapahenerophyte; N, nanophanerophyte; Ch, woody chamaephyte; C, herbaceous chamaephyte; H, hemicryptophyte; G, geophyte; T, therophyte; AN, anemochore; EN, endozoochore; EP, epizochore; MY, myrmechochore; AU, autochore; B, barochore; CSR, intermediate strategists; SR, ruderal stress tolerators.

Table 3
Mean values of Ellenberg indicator values for the forest communities studied

	L	T	F	R	N
Invaded forest	4.8 a	5.3 a	5.6 a	5.6	5.4 b
Managed forest	4.4 b	5.2 b	5.5 b	5.8	5.5 a
Old-growth forest	4.3 b	5.2 b	5.3 c	5.6	5.2 b

Means bearing the same letter are not significant at the level of 0.017 (Kruskal–Wallis test followed by Mann–Whitney *U*-test with Bonferroni correction).

Table 5
Results of the CCA with cover-abundance of *Carex brizoides* and *Impatiens parviflora* as constraining variables

	λ	r	p	Length of gradient
Presence/absence of species		0.93		3.56
Cover of *C. brizoides*	0.26		0.002	
Cover of *I. parviflora*	0.18		0.016	
Cover-abundance of species	0.37	0.91		3.58
Cover of *C. brizoides*	0.37		0.022	
Cover of *I. parviflora*	0.23		NS	

Explanations: eigenvalue (λ) corresponds to the first CCA axis, *r* indicates species–environment correlations, *p* denotes the significance of differences in species composition in the presence of *C. brizoides* and *I. parviflora*. Gradient length corresponds to the first DCA axis.

light availability as indicated by Ellenberg L values. Although Dzwonko and Loster (2000) suggest caution in interpreting the Ellenberg indicator system for recent woods, in this case it accords with evidence of thinner tree cover enabling light to penetrate to the field layer. The higher soil temperature and nitrogen content there, indicated by Ellenberg values in this study, are also associated with increasing light availability, because the latter enhances microbial activity and nitrogen mineralization. This creates favorable conditions for nitrophilous and thermophilous species (Falkengren-Grerup and Tyler, 1991; Dzwonko and Gawronski, 2002). Invaded forest turned out to be the most species-poor according to the species richness scores and Shannon–Wiener indices.

Controversy about the relationship between native and alien species diversity has persisted through the decades. Some studies present negative relationships (Tilman, 1997; Knops et al., 1999; Kennedy et al., 2002) and other works report positive relationships (Lonsdale, 1999; Meiners et al., 2004). Most of these studies concern grassland communities (Tilman, 1997; Knops et al., 1999; Kennedy et al., 2002) or abandoned fields (Meiners et al., 2004). There are almost no such studies devoted to woodland communities except for some related works (Godefroid et al., 2005; Chmura and Sierka, 2005, 2006). Some authors point out that results can vary depending on the level examined. At a regional level, relationships between native and alien species are positive (Levine, 2000; Levine and D'Antonio, 1999; Stohlgren et al., 1999) but at the ecosystem or community level they may be positive or negative (Tilman, 1997; Kennedy et al., 2002; Meiners et al., 2004).

There is much evidence that logging, soil disturbance, thinning of tree stands and above all forest road networks promote invasions of forest interiors (Brothers and Spingarn, 1992; Medwecka-Kornaś, 1994; cf. Noss, 2001). Forest management often involves intentional cultivation of introduced alien plants, and apart from that it generally encourages invasions. Watkins et al. (2001) reported the highest richness/ variability of exotics in the immediate vicinity of forest roads, whereas native species richness and H' was lower there. The lower number of species in invaded forests is probably due to the presence of sedge *C. brizoides*, which hinders the establishment of seedlings and successfully outcompetes many other species (Faliński, 1986; Dzwonko and Gawronski, 2002), finally leading to species impoverishment.

4.2. Ecology of invasive species in the study areas

With a dense layer of *C. brizoides* present, only strong competitors occur, such as *P. aquilinum*, *Rubus* spp. and *U. dioica*, along with the seedlings of many shrubs and trees. The higher the coverage of sedge, the more nonwoodland species there are. The occurrence of young trees and of dwarf shrubs such as blackberry has been described as fruticetization (Olaczek, 1974, cf. Łaska, 2001); it is a type of disturbance of a forest community which results mostly from management practices, especially the thinning of tree stands. According to Dzwonko (2001), *C. brizoides* is a very frequent woodland species in some parts of Poland, and its frequency does not differ significantly between ancient and recent forests, although the species is more abundant and forms denser layers in planted woods (Dzwonko and Gawroński, 1994) and in more open recent woods (Dzwonko, 1993). A long-term experiment with transplantation of *C. brizoides* mats into *Tilio–Carpinetum*-type patches in the Białowieża Forest (Faliński, 1998) confirms that this plant reduces the cover, growth and vitality of all herb species as well as tree seedlings. The origin of the forest, old-growth forest in this case, seems not to be an essential factor. The invasion success of *C. brizoides* results from its very high competitive ability. This study showed that species such as *Galium odoratum*, *Maianthemum bifolium*, *V. reichenbachiana* and *Galeobdolon luteum* do not occur at sites where *C. brizoides* occurs massively, as also demonstrated by Faliński (1998). At such sites the growth and vitality of these species are inhibited at an early stage or during the vegetative period in the presence of the sedge. The other species, small balsam *I. parviflora*, is a very frequent woodland neophyte distributed on a national scale, mainly in the forests of Poland (Tokarska-Guzik, 2005), and widely distributed throughout the forest vegetation of Central Europe (Pyšek et al., 1998). In a sowing experiment (Graae et al., 2004), *I. parviflora* turned out to be almost equally abundant and frequent in both ancient and recent forests. In new oak forests there were no distinct differences between isolated and nonisolated stands (Graae et al., 2003), unlike beech, in which *I. parviflora* was more abundant in new forest stands. Many phytosociological studies have found that the highest preference of *I. parviflora* was for oak–hornbeam forests (cf. Kujawa-Pawlaczyk, 1991; Obidziński and Symonides, 2000; Chmura and Urbisz, 2005). Although its impact on native plants is considered harmful (competitiveness with *I. noli-tangere*) (Trepl, 1984), the effect is not as strong as in the case of *C. brizoides*. Recent work suggests that *I. parviflora* colonizes sites on the forest floor with higher native species richness (Chmura and Sierka, 2006). In terms of spatial pattern, in the literature there is usually a negative correlation between its coverage and the percentage cover of neighboring species, meaning that its abundance is suppressed by competitive plants; in terms of temporal pattern, the role of small balsam in the ground layer usually increases. Due to its competition with native *I. noli-tangere*, Faliński (1998) treated the influence of

small balsam on indigenous components of a community as a supplementary relationship, because the species finally excluded native balsam from the herb layer. According to Kujawa-Pawlaczyk (1991), however, who compared the number of accompanying species on two transects differing in the time at which *I. parviflora* became established, *I. parviflora* exerted a negative influence on neighboring plants, or else a reductive relationship *sensu* Faliński (1998). On the earlier-colonized transect the percentage cover of *I. parviflora* was higher and the number of native species lower than on the transect colonized later. That study did not examine whether changes in species composition and decreases in species richness were due to the competitive ability of *I. parviflora* (i.e., use of nutrient, light and space resources), or rather were due to disturbances facilitating the penetration and spread of this species. In view of the behavior of small balsam, the second explanation seems more probable. The penetration and establishment of small balsam in woodlands is enabled by the following factors: propagule pressure from specimens growing in communities bordering forests, irradiance, gaps in the herb layer (Coombe, 1956; Trepl, 1984; Eliáš, 1999; Obidziński and Symonides, 2000), the presence of wood debris, and rooting by wild boar *Sus scrofa* (Piskorz and Klimko, 2001). All but the last two factors result from forest management practices (Medwecka-Kornaś, 1994). The interplay between nutrient availability and irradiance influences growth and biomass allocation more than it influences abundance, and is not completely understood. Peace and Grubb (1982) concluded that higher mineral availability permits a plant to persist at lower levels of irradiance, but Elemans (2004) did not confirm this. In our study, we indirectly showed the relationship between the presence of *I. parviflora* and higher availability of light. The relationships between increasing abundance of expansive woodland weeds (the case of *Calamagrostis epigejos*) and the light gradient were examined in detail elsewhere (Sierka and Chmura, 2005).

5. Conclusions

Comparison of the obtained data with Sokołowski's (1993) data from old-growth forest shows that there is a gradient of naturalness from old-growth forest to recent and then invaded forests. Some changes are gradual, others not. Penetration of photophilous and forest-edge species is usually caused by thinning of tree stands, opening of canopy gaps, and disturbance of the soil. Though it is impossible to avoid all these changes in the course of forest management in commercial forests, their impact can be minimized. Stands of deciduous trees should be protected especially, but this is difficult to achieve. Remnants of natural forest vegetation are characterized by higher resistance to invasion; as many studies show, such vegetation hampers or even stops the further spread of invasive species. In the absence of such stands, the usual nature conservation practices are not enough. Only active protection is effective.

Our study showed that of the two invasive species, *C. brizoides* is a better indicator of human-induced disturbance.

As a light-demanding species and a clonal plant, it gains more benefit from thinning and cutting of tree stands.

Forestry practices to limit the massive expansion of *C. brizoides* include draining of land or whitewashing of soil. Motyka (1947) suggested that its negative influence on seedlings of trees such as *Quercus robur* and *Q. petraea* could be reduced by planting young trees on hillocks beyond the range of *C. brizoides* rhizomes. Becker and Levy (1983) discussed its benefit in ecological terms, but the efficacy of such a procedure has not been demonstrated in practice. *I. parviflora* has a natural enemy, the rust *Puccinia komarovi*, which causes high mortality in populations of the species (Bacigalova et al., 1998). This fungus could be used as a biological control. Other methods such as hand-weeding of the plants are effective only at the beginning of an invasion (Csontos, 1986; Adamowski and Keczyński, 1998).

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