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Sustainable autochthonous forest ecosystems as natural barriers to the spread of invasive alien species

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Abstract. An analysis of the quantitative participation of invasive alien species (IAS) in main types of natural forests in Bulgaria and artificial plantations with the participation of native and exotic species was carried out. The object of study are forest phytocoenoses in 62 permanent sample plots (PSP) on the territory of the country part of the network for large-scale monitoring ICP Forests, located at an altitude between 250 and 1800 m above sea level. The study was conducted in the period 2019-2023 and covers 4 of the regions of the monitoring network as follows: II - Sredna Stara Planina (northern slopes) (15 PSPs), IV A - Sredna Stara Planina (southern slopes) and Sredna Gora (eastern part) (10 PSPs), V - Osogovo, Kraishte, western slopes of Rila and Vitosha (19 PSPs) and VI - Mountains in Southwestern Bulgaria (18 PSPs). The results show that limiting the spread of invasive alien species in forest ecosystems is largely influenced by the degree of their autochthony, the pronounced vertical structure, the high canopy of the trees layer, good regeneration, health status and control over the anthropogenic factor. Most IAS are heliophytes and the high coverage of the trees layer prevents their penetration. Many of the native species characteristic of our forests are highly competitive with IAS with their adaptations for vegetative reproduction (via root and stem shoots) and allelopathic properties, which in natural forest ecosystems form a specific microclimate and background of biologically active substances that repel IAS.

Key words: exotic species, native communities, artificial plantations.

Introduction

The functional types of invasive alien species (IAS) are considered to have a negative impact on forest integrity (Mavimbela et al., 2018). Understanding the spatial pattern of invasive species and disentangling the biophysical drivers of invasion at forest stand level is essential for managing invasive species in forest ecosystems and the wider landscape (Sharma et al., 2023). IAS invasion in forest is now increasingly being recognized as a global problem, and various continents are adversely affected, although to a differential scale (Rai, 2015). Understanding how forests respond to IAS in the light of global change is critical to forest conservation, climate protection and sustainability of biodiversity and ecosystem services and this implies the need for worldwide forest monitoring (Anderson-Teixeira et al., 2015).

Since 1986 Bulgaria has been part of the International Cooperative Program on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests). The focus of the Program today is also on other factors influencing forests, such as climate change, biodiversity loss, prolonged droughts, IAS, etc. (Executive Environment Agency, 2023). The scientific and research activity on ICP-Forests is carried out by two collectives - of the University of forestry and the Forest Research Institute - BAS. 10 regions with conditional borders were adopted, in which different types of activities are performed annually (Pavlova & Rosnev, 2006). The implementation of the Program provides information on a large number of indicators for sustainable forest management, defined by the Ministerial Conference on the Protection of Forests in Europe, the United Nations Framework Convention on Climate Change and the Convention on Biological Diversity (Pavlov & Glogov, 2021)

The aim of the present study is to analyze the spread of IAS in the plant communities within the ICP-Forest monitoring network on the territory of the country.

Materials and methods

The objective of study are forest phytocoenoses of artificial and natural origin in 62 permanent sample areas (PSPs) of ICP Forests, located at an altitude between 250 and 1800 m a.s.l. The study covers 4 of the regions of the monitoring network as follows: II - Sredna Stara Planina (northern slopes) (15 PSPs), IV A - Sredna Stara Planina (southern slopes) and Sredna Gora (eastern part) (10 PSPs), V - Osogovo, Kraishte, western slopes of Rila and Vitosha (19 PSPs) and VI - Mountains in Southwestern Bulgaria (18 PSPs) (Fig 1).

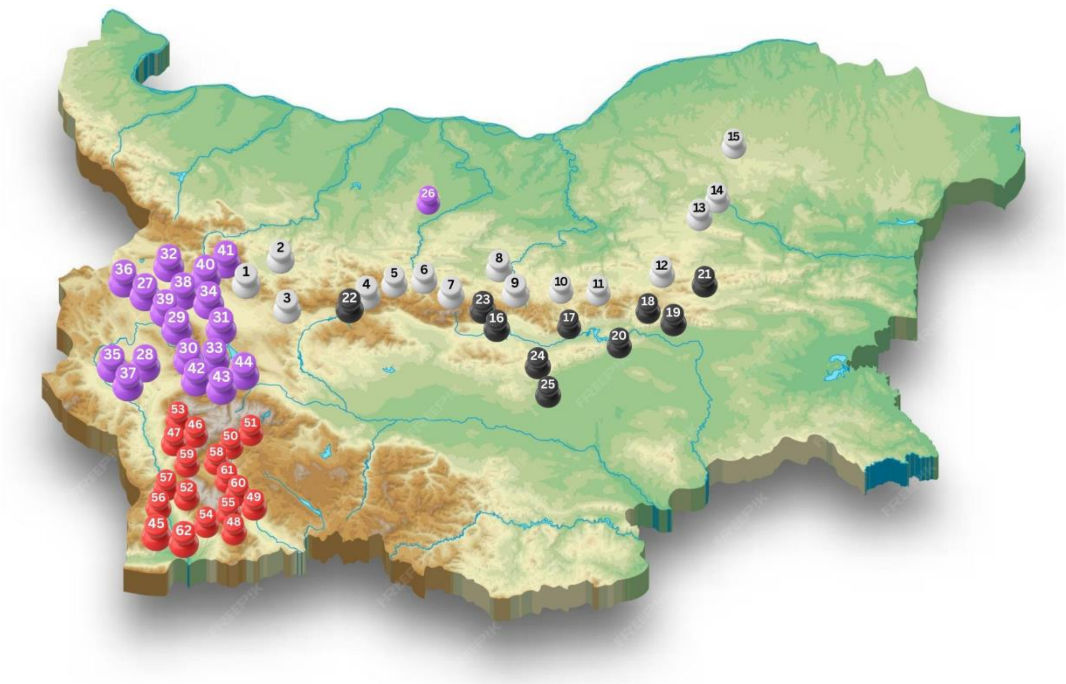

Fig. 1. Locations of the PSPs by regions (numbers and colors): II (1-15, white), IV (16-25, black), V (26-44, purple), VI (45-62, red). For more details, see Legend to Table 1.

The study was conducted in the period 2019-2023. The Assessment of vegetation is done according to Chapter VII of the ICP Forests Manual (Canullo et al., 2020). PSPs for monitoring forest ecosystems fall at the intersections of 16 × 16 km, 8 × 8 km and 4 ×4 km grids. The size of the PSP depends on the composition, age and completeness of the stands and varies from 875 to 2000 m^2.

For the needs of the analysis, the following data were established from each PSP: main tree species (edificator), type of plantation (artificial or natural), altitude, coverage (%) of the phytocoenotic layers, composition and coverage (%) of invasive alien species (IAS) and alien species (AS). Rav (%) is the ratio of the number of autochthonous species to the total number of species (autochthonous, anthropophytes, apophytes, secondary elements, etc.) in each PSP.

The anthropogenic impact on the plantations was assessed on a three-level scale depending on the frequency of human interventions and their results such as felling, collecting herbs, etc., the presence of waste, traces of anthropogenic activity incl. clearings, roads, etc. in the immediate vicinity of the PSP, as follows: 1 - small anthropogenic impact; 2 - medium anthropogenic impact; 3 - strong anthropogenic impact.

A beta-regression model was applied to analyze the data for the presence of invasive species, reported as fractional cover (i.e. in the interval (0,1)) in 62 PSPs. The calculations were implemented with the betareg library from the R platform, presented in Zeileis et al. (2014). Previously, where necessary, the transformation required by the beta-regression model was applied to this type of data (Smithson & Verkuilen, 2006).

Results

The survey data (Table 1) show that the ratio (in %) of artificial to natural plantations in the PSP is 29.71%. The distribution of PSP by edificators is as follows: *Fagus sylvatica* L. – 29.0%; *Pinus sylvestris* L.- 22.6%; *Pinus nigra* Arn.- 16.1%, *Picea abies* (L.) Karsten.-11.3%; *Quercus cerris* L.- 8.1%; *Carpinus betulus* L- 4.8%; *Quercus dalechampii* Ten.- 4.8%; *Quercus frainetto* Ten.-3.2%.

Table 1. Survey data

PSP No	Edificator	ToP	Altitude (m)	Tree cover (%)	Shrub cover (%)	Herb cover (%)	Moss cover (%)	Rav (%)	Anthropogenic impact (Ai)	IAS cover (%)	AS cover (%)
1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
1	*C.b.*	2	918	90	5	35	2	98	1	0	0
2	*Q.d.*	2	783	80	30	35	1	100	1	0	0
3	*F.s.*	2	768	50	60	40	5	98	1	0	0
4	*F.s.*	2	1100	80	1	20	1	97	1	0	0
5	*F.s.*	2	670	80	5	10	3	91	1	0	0
6	*F.s.*	2	478	70	10	35	5	100	1	0	0
7	*P.s.*	1	575	50	40	40	1	76	2	2	0
8	*Q.c.*	2	340	50	50	30	1	90	1	0	0
9	*P.n.*	1	475	65	30	30	4	80	1	0	0
10	*Q.d.*	2	306	70	55	30	1	100	1	0	0
11	*F.s.*	2	460	75	20	40	1	98	1	0	0
12	*F.s.*	2	710	45	70	65	2	86	3	0	0
13	*F.s.*	2	315	90	15	20	1	97	1	0	1
14	*Q.f.*	2	250	40	65	50	0	92	1	0	0
15	*C.b.*	2	400	75	45	70	1	98	1	0	0
16	*P.s.*	1	355	70	40	70	5	70	1	12	0
17	*Q.d.*	2	465	80	15	60	1	95	1	0	0
18	*Q.c.*	2	450	70	30	40	3	82	1	0	0
19	*F.s.*	2	1025	75	35	40	3	94	1	0	0
20	*Q.f.*	2	400	70	20	50	1	78	1	0	0
21	*F.s.*	2	760	70	50	40	1	94	1	0	0
22	*P.s.*	1	1080	50	65	20	0	76	1	0	0
23	*F.s.*	2	950	90	20	50	3	94	1	0	0
24	*Q.c.*	2	398	70	35	65	1	89	1	0	0
25	*Q.c.*	2	535	50	60	70	3	91	1	0	0
26	*P.s.*	1	971	75	10	13	20	82	1	0	2
27	*P.n.*	1	1092	65	30	25	5	64	1	0	30
28	*P.n.*	1	726	65	45	55	5	68	2	40	0
29	*P.s.*	1	778	65	65	35	0	83	1	0	0
30	*P.s.*	1	809	70	55	65	5	79	2	35	0
31	*P.s.*	1	838	70	35	30	5	78	2	7	5
32	*P.n.*	1	672	85	15	5	5	91	1	0	0
33	*P.n.*	1	951	80	20	30	1	78	2	5	0
34	*P.n.*	1	835	70	85	45	1	77	2	3	0
35	*P.n.*	1	836	70	15	35	2	79	1	0	0
36	*F.s.*	2	1040	55	25	40	5	100	1	0	0
37	*F.s.*	2	1589	65	35	65	1	97	1	0	0
38	*F.s.*	2	863	65	30	35	0	98	1	0	0

39	*C.b.*	2	867	80	25	40	0	98	1	0	0
40	*Q.c.*	2	965	75	30	70	0	84	2	0	0
41	*P.s.*	1	1298	75	60	60	0	88	1	0	0
42	*P.a.*	2	1307	80	5	45	4	98	1	0	0
43	*P.s.*	2	1302	70	35	50	0	100	1	0	0
44	*P.a.*	2	1574	65	7	55	12	100	1	0	0
45	*P.n.*	1	320	75	40	60	5	80	1	0	0
46	*P.a.*	2	1473	60	20	20	10	100	1	0	0
47	*P.s.*	2	802	60	30	40	5	88	1	0	0
48	*P.s.*	2	1180	70.	50	30	5	90	1	0	0
49	*P.n.*	1	647	55	35	45	20	61	2	5	0
50	*P.s.*	2	1590	70	40	45	10	100	1	0	0
51	*P.a.*	2	1600	85	15	20	5	100	1	0	0
52	*P.s.*	2	1490	70	25	40	5	93	1	0	0
53	*F.s.*	2	1492	70	20	35	20	100	1	0	0
54	*F.s.*	2	1214	80	5	10	10	100	1	0	0
55	*F.s.*	2	1150	85	30	15	10	100	1	0	0
56	*F.s.*	2	1080	70	15	10	5	100	1	0	0
57	*P.n.*	1	785	85	15	5	5	95	1	0	0
58	*P.s.*	2	1372	70	20	50	5	100	1	0	0
59	*P.a.*	2	1180	65	40	30	25	100	1	0	0
60	*P.a.*	2	1387	75	60	40	10	100	1	0	0
61	*P.a.*	2	1670	75	0	60	25	100	1	0	0
62	*F.s.*	2	1180	80	15	15	5	88	1	0	3

Legend to Table 1:
Column 1 - PSPs (No, name of the locality, coordinates):
Region II: 1. Churek, 42°47'26.9"N 23°43'46.0"E; 2. Zelin, 42°52'25.4"N 23°50'07.2"E; 3.Etropole monastery, 42°49'25.5"N 24°02'04.0"E; 4. Ribaritsa, 42°51'47.2"N24°29'04.6"E, 5. Shipkovo, 42°52'42.7"N 24°35'36.9"E; 6. Kapincho, 42°53'01.8"N 24°43'27.1"E; 7. Boaza, 42°53'40.4"N 24°57'25.3"E; 8. Vishovgrad, 43°08'23.2"N 25°17'14.4"E; 9. Gostilnitsa, 43°01'49.9"N 25°22'13.7"E; 10. Shemshevo, 43°03'27.3"N 25°32'28.3"E; 11. Plakovo, 42°55'40.2"N 25°42'40.4"E; 12. Gorsko selo, 43°02'19.6"N 26°21'26.3"E; 13. Prolaz, 43°11'44.6"N 26°30'06.3"E; 14. Ralitsa, 43°18'40.4"N 26°30'06.6"E; 15. Pchelin, 43°27'57.3"N 26°27'58.1"E;
Region IV: 16. Koprinka dam, 42°36'26.0"N 25°18'47.8"E; 17. Pchelinovo, 42°44'11.6"N 25°42'22.4"E; 18. Medven, 42°50'49.2"N 26°31'25.2"E; 19. Karandila 42°45'00.9"N 26°20'41.8"E; 20. Nova Zagora, 42°34'47.2"N 25°55'09.6"E; 21. Demir kapia, 42°51'47.3"N 26°28'47.6"E; 22. Klisura, 42°42'25.9"N 24°23'13.6"E, 23. Shipka, 42°44'06.5"N 25°19'30.8"E; 24. Starozagorski mineralni bani, 42°27'14.4"N 25°29'17.8"E; 25. Chirpan, 42°16'26.0"N 25°26'00.2"E;
Region V: 26. Lisetz, 43°10'59.7"N 24°39'53.8"E; 27. Breznik, 42°43'54.7"N 22°54'32.0"E; 28. Nevestino, 42°15'07.6"N 22°51'06.1"E; 29. Radomir, 42°32'39.0"N 22°56'22.6"E; 30. Ovchartsi, 42°16'11.9"N 23°13'33.3"E; 31. Dren, 42°23'35.5"N 23°08'35.5"E; 32. Aldomirovtsi, 42°51'29.1"N 22°59'31.3"E; 33. Klisura, 42°19'40.8"N 23°21'43.8"E; 34. Gorna bania, 42°39'50.1"N 23°12'55.6"E; 35. Hisarluka, 42°16'27.4"N 22°41'21.4"E. 36. Zavala, 42°49'28.0"N 22°48'05.3"E; 37. Tri buki, 42°10'50.7"N 22°37'18.2"E; 38. Mihailovo, 42°40'59.7"N 23°07'10.9"E; 39. Malo Buchino, 42°40'26.1"N 23°09'24.2"E; 40. Vladaia, 42°38'19.7"N 23°11'05.3"E; 41. Selimitsa, 42°34'15.2"N 23°14'19.8"E; 42. Lakatitsa,42°15'56.2"N 23°28'35.0"E; 43. Nataritsa, 42°14'29.8"N 23°25'50.5"E; 44. Ovnarsko, 42°13'25.9"N 23°25'15.4"E;
Region VI: 45. Samuilovo, 41°22'18.2"N 23°05'00.4"E; 46. Parangalitsa, 42°02'25.1"N 23°22'19.5"E 47. Gorno Harsovo, 42°00'44.6"N 23°12'02.7"E; 48. Papaz Chair, 41°34'02.3"N 23°39'21.8"E 49. Garmen, 41°36'44.4"N 23°48'33.1"E; 50. Yakoruda, 42°01'20.6"N 23°39'44.7"E; 51. Leeve, 42°06'02.0"N 23°42'21.0"E; 52. Turichka cherkva, 41°40'01.8"N 23°23'54.7"E; 53. Rila Monastery, 42°08'02.1"N 23°20'21.3"E; 54. Katuntsi, 41°26'41.2"N 23°25'52.0"E 55. Gotse Delchev, 41°34'14.8"N 23°39'45.8"E; 56. Studenata voda, 41°36'57.3"N 23°01'59.0"E; 57. Tsaparevo, 41°36'36.4"N 23°05'58.8"E; 58. Belitsa, 41°57'12.7"N 23°33'11.9"E; 59. Predela, 41°52'32.2"N 23°20'43.6"E; 60. Dobrinishte, 41°45'32.8"N 23°33'36.3"E; 61. Bansko, 41°49'19.1"N 23°29'47.8"E; 62. Kongura, 41°21'56.4"N 23°11'44.7"E.
Column 2 - Edificator (main tree species): C.b.- *Carpinus betulus*; Q.c.- *Quercus cerris*; Q.d.- *Quercus dalechampii*; Q.f.- *Quercus frainetto*; F.s.- *Fagus sylvatica*; P.s.- *Pinus sylvestris*, P.n.- *Pinus nigra*, P.a.- *Picea abies*.
Column 3 - Type of plantation: 1- artificial; 2- natural;

Within the PSPs in the studied forest phytocoenoses, two tree IASs were established - *Robinia pseudoacacia* L. (with coverage between 5 and 40% in the PSP) and *Laburnum anagyroides* Medicus (coverage 2-5%), and one herbaceous plant - *Erigeron annuus* (L.) Pers (coverage 1-2%). Other alien species registered in the PSPs are *Pseudotsuga menziesii* (Mirb.) Franco (1-2%), *Quercus rubra* L. (5-30%), *Mahonia aquifolium* (Pursh) Nutt. (2-10%).

Regarding the spread of IAS in forests, the studied factors were ToP (type of plantation, p = 0.07), the coverage of the herbs layer (herb, p = 0.06), the exceeding of the second level of anthropological impact above the first and third (Anthropolog. Impact, p = 0.0003). The statistical significance of the factors from the ANOVA-table determines the further course of the analysis and the corresponding conclusions. The type of plantation (ToP) turns out to be a feature that differentiates the occurrence of IAS. There are a total of 8 PSPs in which a greater or lesser presence of IAS was reported. They represent 13% of all PSPs and 44% of PSPs with artificial plantations (18 in number). No invasive species were reported in the PSPs with natural plantations (44 in number) (Fig. 2).

The cover of the third layer (the herbs layer) with the reported presence of IAS is at the level of the generally accepted limit for statistical evidence due to the overlap of a certain part of the interquartile range (IQR) of the herbs coverage in the sample areas in the presence and absence of IAS (Fig. 3). The study shows that a greater coverage of herb layers in forest communities predisposes to the penetration of IAS.

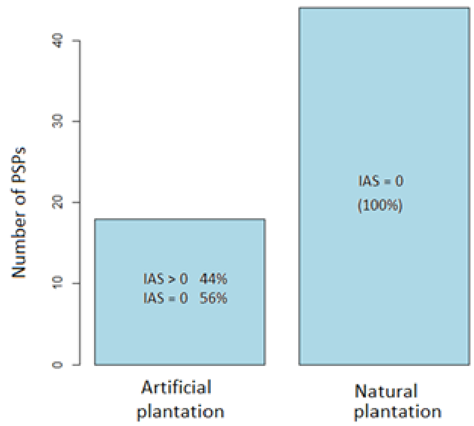

Fig. 2. Relative distribution of PSPs by type of plantation. Participation (%) of IAS

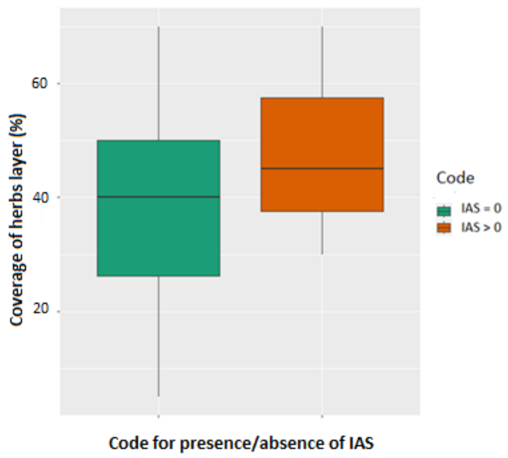

Fig. 3. The distribution of herb cover abundance (%) depending on the presence of the IAS in the PSPs.

Anthropogenic impact is coded with three levels (corresponding to the ratings) “1, 2 and 3” in ascending order. The influence of anthropogenic impact on the presence of IAS has been statistically proven. The percentage presence of IAS in the anthropogenically unaffected sample areas is below 2% of their number. The same percentage for the anthropogenically affected sample areas around 78%. The distribution of the PSPs according to the levels of anthropogenic impact is as follows: 55 PSPs in which a small anthropogenic impact was found (with a rating of 1); 6 PSPs with medium anthropogenic influence (rated 2); 1 PSP with strong anthropogenic influence (rated 3).

With a third level of anthropogenic impact, only one PSP was reported, which was joined to those with a second level, then the distribution of PSPs by levels of anthropogenic impact with noted percentage presence of IAS is as follows: 55 PSPs with assessment 1; 7 PSPs with a score of 2. Therefore, medium and high levels of anthropogenic impact have been statistically proven to increase the presence of IAS (Fig 4).

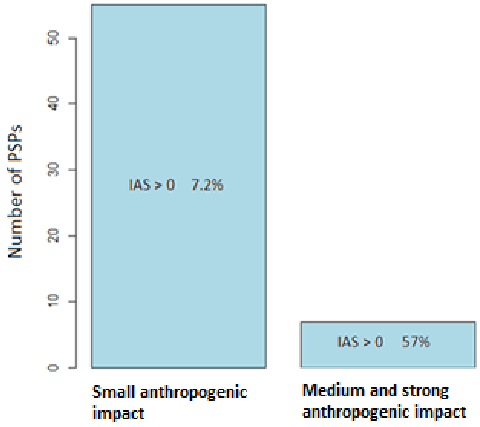

Fig. 4. Relative distribution of the number of PSPs according to the presence of anthropogenic impact with IAS reported presence (%) included.

Alien (non-invasive) species (AS) were present in only 4 PSPs and for them the beta-analysis did not report a statistically significant influence of any of the factors included in the data.

The influence of altitude (Alt - Altitude), coverage of trees layer, shrubs layer, mosses layer and the Rav index is statistically unproven. Since, according to other studies (Martin et al, 2009; Gómez et al., 2019), some of these indicators play an important role in the prevalence of IAS, in addition, a graphical representation of the presence of IAS grouped by the ABC-classification was made (Thrum et al., 2017) and the values of the corresponding feature on a common graph. Its abscissa is the trait values, and the coverage of IAS is plotted on the ordinate. For altitude (Alt), the graph obtained using the ggplot2 package (Wickham, 2016) has the following appearance (Fig. 5):

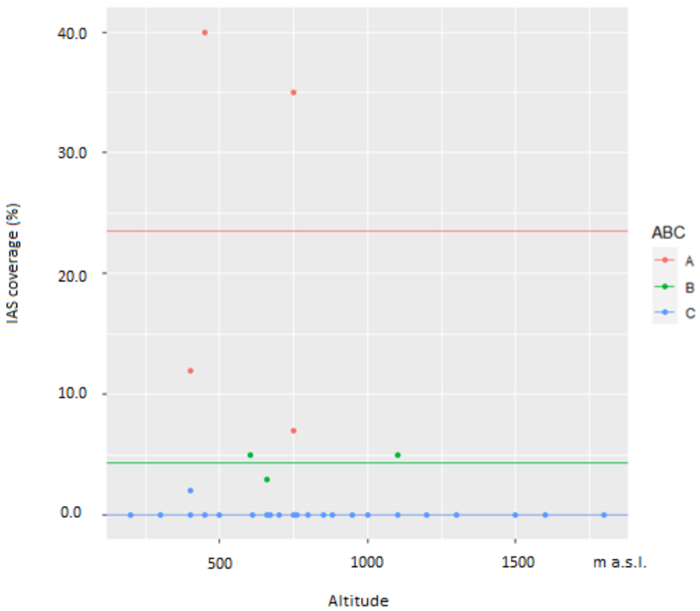

Fig. 5. Coverage of IAS depending on altitude with labeled ABC-grouping.

The graph in Fig. 5 shows that what is indicated as high coverage of IAS (group A) occurs at altitudes up to about 800 m, where 2 of the three test areas with medium coverage are located. At higher values of the altitude, the presence of IAS is not considered. The available data do not allow this conclusion to be considered as statistically proven, but only as subject to subsequent verification.

For the tree layer coverage feature (trees coverage), the graph is as follows (Fig. 6):

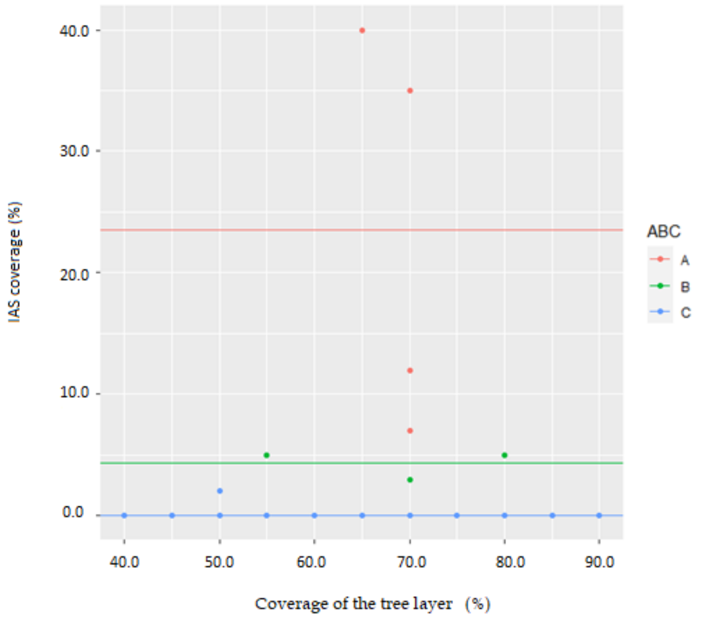

Fig. 6. Coverage of IAS in relation to the coverage of the tree layer with designated ABC grouping.

The high values of IAS (group A) are located approximately in the interval 65-70% coverage of the trees layer. The second group of IAS extends this interval. With coverage of tree layers below 55% and above 80%, no IAS were recorded. In the coverage of shrub layers, the picture is similar, but the groups are not as clearly distinguishable as in the tree layer coverage.

The presence of native species in the forest plantations is generally high, with a cover between 80 and 100% occurring in the natural stands of spruce, scots pine, beech, hornbeam and oak, where, despite the absence of IAS, it is sporadically observed entry of secondary and pioneer species such as *Pteridium aquilinum*, *Populus tremula*, *Juglans regia*, etc., often as a result of natural disturbances (windstorms, etc.) or illegal logging. In the artificial phytocoenoses of *Pinus nigra* and *P. sylvestris*, the percentage of autochthonous species is lower (60-85%), and there along-side IAS such as *Robinia pseudoaacacia*, *Laburnum anagyroides*, etc., established secondary tree and shrub species (incl. apophytes) such as *Paliurus spina-christi* Mill., *Prunus spinosa* L., *Prunus cerasifera* Ehrh., etc., and a number of anthropophytes such as *Eringium campestre* L., *Tanacetum vulgare* L., *Cichorium intibus* L., *Euphorbia cyparissias* L., *Taraxacum officinale* (L.) Weber ex F.H.Wigg., *Cirsium vulgare* (Savi) Ten., *Mellilothus officinalis* (L.) Pall., *Acinos arvensis* (Schur) Dandy, *Ajuga genevensis* L., *Daucus carotta* L., *Achillea millefoilum* L., etc. For the feature related to the presence of autochthonous species in the phytocoenoses (Rav), the location of the points is grouped much more distinctly (Fig. 7).

All sample areas with reported presence of invasive species have Rav < 80%. For Rav values > 80% no invasive species are considered.

Discussion

The appearance of alien plant species, incl. the invasive ones are mainly due to negative human intervention and the proximity of plantations of such species (*Quercus rubra*, *Robinia pseudoaccacia*, *Pseudotsuga menziesii*).

Foreign species in phytocenoses attract other foreign species, changing the water-physical and chemical properties of the soil, the natural microclimate (including at the level of allelopathic influences), as well as the habitat as a whole (Early et al., 2016).

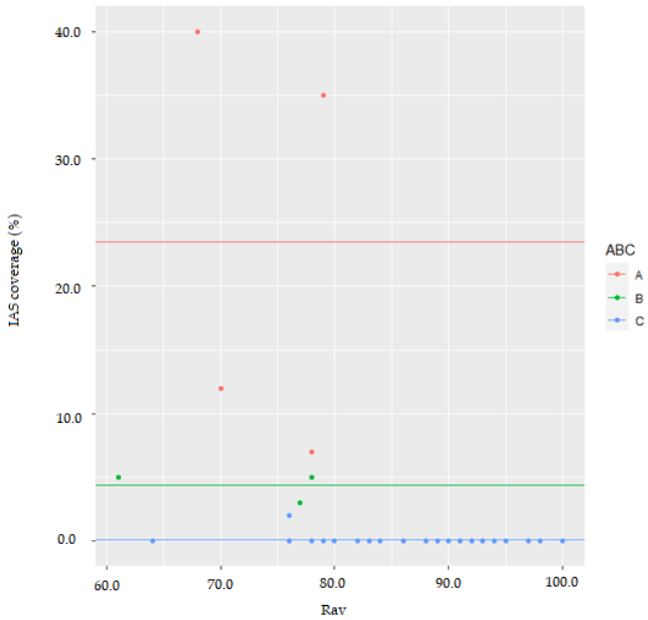

Fig. 7. Coverage of IAS depending on the ratio Rav with labeled ABC-grouping.

Role of plantation types and their edificatory species on the spread of IAS in the PSPs

According to Hejda et al. (2009) the effect on community characteristics is determined by the character of the invaded community, especially the dominance of the native dominant relative to that of the invader. The results of an up-to-date analysis of Popov et al. (2018) show that the edificators *Pinus nigra* and *P. sylvestris* in artificial plantations in the xerothermic oak zone are outside their natural range and often suffer from water deficits, making them uncompetitive, both with native and invasive alien species. In artificial stands, the risk of deterioration of the health status of trees is increased, which is also a factor favoring the entry of IAS (both plants and insects and fungi, etc.). In some of the specific PSPs (No. 3 and No. 5), a threat to natural diversity is represented by *Robinia pseudoaccacia*, which dominates the second layer and could easily become an edificator species after removing the pine plantation.

The established relationship between the type of plantation and the spread of IAS confirms the findings of Moore (2005) that the conversion of natural forest to artificial stands, can have direct and indirect negative impacts on the ecological functions of forests and on forest biodiversity by promoting the invasion of alien species. It also confirms observations of Zerbe & Wirth (2006), which found that tree stands of *Pinus sylvestris* host numerous alien species, including many invasive species. The authors consider that taking into account that a high proportion of the investigated pine forests is of anthropogenic origin and will naturally develop towards broad-leaved forests with beech and oak, it is hypothesised that most of the observed invasions are reversible.

The invasion of IAS in artificial forest communities is a sign of a different degree of development of succession processes in them, the causes of which are external (climatic changes, anthropogenic impacts) and internal (result of interactions between species and their environment inside the community) (Prach & Walker, 2011). For the most part, the habitats where the pine stands were created are not typical for them, which makes them vulnerable to the impact of climatic factors such as drought, pests and pathogens (Popov et al., 2014, 2018). Artificial forest stands are secondary communities, anthropogenically influenced, they carry some of the characteristics of the original phytocoenoses, but in many respects they differ from them. Such differences are observed in their structure - such as a rarer canopy, monodominance of the first layer, which facilitates competition in the lower layers, in addition to the species characteristic of the indigenous communities, the floristic composition of the artificial stands includes many evribiont species – cosmopolitans, pioneer species, ruderals. Many free niches are found in them, including for IAS, which usually settle along forest roads and forest edges.

A positive correlation between anthropogenic impact and the spread of IAS in forest communities is an expected result. Anthropogenic disturbances like overgrazing, indiscriminate and uncontrolled tree felling, and habitat fragmentation cause severe stress on forests which further increase the susceptibility to invasion (Saharan et al., 2021). Clearing may change light conditions and resource availability in ways that favour alien plant species (Langmaier & Lapin, 2020). Human activities increase the risk of secondary successions and ruderalization of forest habitats, open pathways for the penetration of IAS and facilitate the direct transfer of their seeds or propagules, through which they can regenerate their populations vegetatively (González-Moreno et al., 2014).

Influence of altitude, coverage and the level of autochthony of the species composition on the spread of IAS in the PSPs

The present study complements and confirms the results of the study on horological data by Glogov (2023) on the distribution of IAS in Bulgarian forests. The latter shows that natural and artificial forest communities in the lower forest vegetation zone are the most threatened in terms of the vertical spread of IAS. With the changes in the country's climatic conditions, in vertical terms, the limit of distribution of IAS will increase, and for some of the most dangerous IAS such as *Ailanthus altissima* (Mill.) Swingle and *Amorpha fruticosa* L., it is currently up to 1500 m.

Measuring coverage is the most feasible option to quantify the impact of invasive species, it is considered a key variable in the biological invasion process because the advantage of monopolizing space in the community to the detriment of native species is directly related to impact (Magalhães et al., 2020). The results of ABC-analysis are consistent with established dependencies from similar studies (Fajardo & Gundale, 2018, Sharma et al., 2023). The lower coverage of the tree layer, combined with other ecological factors, facilitates the entry of light-loving species, which most IAS are. The prerequisites established in the present study for the entry of IAS into communities with a higher coverage of the herbs layer can be explained on the one hand by the changes in lighting occurring under the canopy of the studied communities. The penetration of more sunlight (in oak and pine forests) increases the number and, accordingly, the coverage of heliophytes, while in beech and spruce communities, where the environmental conditions are suitable for shade-loving species, the composition and quantitative participation of grass species is more limited, incl. regarding the presence of IAS. Another explanation is the undergrowth of tree and shrub species (including IAS) involved in the herbs layer, which in some stands has the predominant cover in the vegetation structure.

The present study demonstrates that a high level of autochthony of forest communities is a prerequisite for their resistance to IAS invasion. In this particular case, the conclusions of a study by Hejda & Pyšek (2006) are confirmed, that the entry of IAS into forests is accompanied by the penetration of local ruderal species.

There are several reasons why the spread of IAS in the monitored communities in PSPs is difficult at this stage. First, a number of invasive species with high coverage in the second and third floors such as *Fagus sylvatica*, *Carpinus betulus*, *C. orientalis*, *Fraxinus ornus*, etc., are registered among the local plants, which are serious competitors of IAS. In all PSPs, good regeneration of native edificator species including *Quercus daleschampii*, *Q. cerris* and *Q. frainetto* was observed in the pine stands. In the natural communities, which for the most part have a three-layer structure, the composition of species typical for the habitats is preserved, which is an indicator of the preservation of the specific microclimate in the phytocoenoses incl. the emission of biologically active substances that suppress the IAS.

Conclusions

The investigation reveal that limiting the spread of IAS in forest ecosystems is largely influenced by the degree of their autochthony, the pronounced vertical structure, the high canopy of the tree layer, the high regeneration of the edificetor species, the good health status and the control over the anthropogenic factor. Most IAS are heliophytes and the high density of the tree layer prevents their penetration, many of the species characteristic of our forests are highly competitive to IAS with their adaptations for vegetative reproduction (via root and stem shoots) and allelopathic properties, which in natural forest ecosystems form a specific microclimate and a back-ground of biologically active substances that repel IAS.

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