Alien and Native Dominants Exercise Similar Effects on the Species Richness in Synanthropic Plant Communities of the Western Caucasus

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Abstract—It remains unclear whether the effect exercised by alien dominants on the species richness in plant communities is on average stronger than the effect exercised by native dominants. To clear up this point, 20 synanthropic plant communities dominated by species of different biogeographical origins were surveyed in the Belaya River valley, Western Caucasus (190–680 m above sea level). For each of the studied communities, aboveground biomass samples were collected on 25–30 plots 0.25 m^2 in size with different shares of dominants; the collected samples were subsequently sorted by species and weighed. Analysis of the field data made it possible to draw the following conclusions: (1) samples with high shares of alien and native dominants differ statistically insignificantly in the average number of species; (2) on average, the relationship between the degree of dominance of alien species and the species richness is as strong as the relationship between the degree of dominance of native species and the species richness; (3) in most cases, the relationship between these parameters can be satisfactorily explained by the "energy–diversity" hypothesis; and (4) the proportion of synanthropic plant species in communities with high shares of alien and native dominants is not higher than that in communities with low shares of these dominants. Overall, the results indicate that alien and native dominants exercise similar and mostly nonselective effects on accompanying species in plant communities.

INTRODUCTION

According to the "energy–diversity" hypothesis (Wright, 1983) and the "larger number of individuals" hypothesis (Srivastava and Lawton, 1998) that explains it, the higher the productivity of habitats, the higher is the total biomass of individuals in areas occupied by communities (and, accordingly, their density), and the higher is the probability that these individuals belong to many species. Field data generally confirm the validity of these assumptions in relation to plant communities, except for situations when communities differ in species pool size and significantly differ in the average height (size) of individuals (Grime, 1973; Garsia et al., 1993; Oksanen, 1996; Zobel and Partel, 2008; Símová et al., 2013).

It also follows from the above hypotheses that the higher is the share of dominants (i.e., the degree of dominance) in a plant community, the less resources remain available for other (associated) species, and the lower are the total biomass and number of such species. This makes it possible to explain the strong relationship between the degree of dominance and the species richness that is often observed in small fragments of phytocoenoses, including synanthropic ones, especially if they belong to the competitive type (CRS organization model) (Mirkin, 1994; Mirkin et al., 2007; Akatov et al., 2018, 2019). This mechanism implies that an increase in the share of dominants leads to a nonselective (i.e., random) elimination of other (associated) species from such sites. Therefore, the impact exercised by dominants may result in a significant decrease in the occurrence frequency of associated species; however, with a certain probability, any of the associated species can be discovered in any fragment of the phytocoenosis with any share of the dominant. This means that species pools of these fragments are approximately the same in size. If so, a certain amount of biomass of associated plant species sampled in fragments of a plant community featuring high shares of the dominant should include roughly the same number of species as a similar amount of biomass sampled from fragments of the same community with low degrees of dominance of this dominant.

However, dominants can also affect associated species in other ways, e.g., by transforming ecotopes (litter accumulation, changes in the light and hydrological regimes, changes in physicochemical soil properties, etc.) or through allelopathy (Rabotnov, 1983; Levine et al., 2003; Callaway and Ridenour, 2004; Reinhart et al., 2005; Csergő et al., 2013; Lanta et al., 2013; Bartha et al., 2014; Gioria and Osborne, 2014; Blackburn et al., 2019). The environment-forming activity of dominants can prevent the growth of some (unstable) species in communities, but have no effect on other (stable) species (selective impact). As a result, the species pool in fragments of phytocoenoses with high degrees of dominance is smaller than on sites with low degrees of dominance. In such cases, a certain amount of biomass of associated plant species sampled in fragments of a plant community featuring high shares of the dominant should include a smaller number of species than a similar amount of biomass sampled in fragments of the same community with low degrees of dominance of this dominant. It can also be assumed that the relationship between the degree of dominance and the species richness in communities in this case should be stronger in comparison with a situation when this relationship is determined only by the amount of resources available to associated species.

One of the consequences caused by the saturation of regions with alien species is that such species become predominant in some phytocoenoses (Rejmánek et al., 2013). This usually happens after severe disruptions in communities (Reinhart et al., 2005; Smith et al., 2009), but apparently other variants cannot be ruled out. For a number of reasons, this process can pose threats to the phytodiversity of recipient regions. First, alien species may be stronger competitors for resources than native species that normally predominate in such habitats and hence reach higher abundance levels. The higher the degree of dominance of alien species, the stronger is their impact on other species (Meiners et al., 2001; Silliman and Bertness, 2004; Hejda et al., 2009; Seabloom et al., 2015). Second, the available data indicate that local plant species can be more resistant to environment-forming effects of native dominants because of their long periods of coexistence (conjugate evolution) compared to alien dominants (Rabotnov, 1983; Meiners et al., 2001; Rejmánek and Simberloff, 2017; Hejda et al., 2017; Blackburn et al., 2019). Finally, some studies indicate that the replacement of native dominants with alien ones often increases the share of synanthropic plants among associated species because of their greater resistance to this factor (Hejda and Pyšek, 2006; overviews: Gusev, 2018; Veselkin and Dubrovin, 2019). As a result, the species composition of communities with low and high shares of an alien dominant can differ significantly (low species similarity) (Hejda et al., 2009).

But does the impact of dominants on the species richness in plant communities really depend on their origin (i.e., whether they are alien or native)? Many studies support this supposition (Richardson et al., 1989; Standish et al., 2001; Akatov et al., 2012; Lanta et al., 2013; Gusev, 2016, 2017, 2018; Hejda et al., 2017; Rijal et al., 2017; Vítková et al., 2017; Blackburn et al., 2019; Veselkin et al., 2020; etc.). However, there is also an alternative opinion: the available data are rarely based on comparisons of representative community samples with dominants of different origins; therefore, despite the importance of this question for conservation practice, there are still insufficient grounds for a positive answer to it (Houlahan and Findlay, 2004; Sagoff, 2005; Davis et al., 2011; Blackburn et al., 2019; Hejda et al., 2021). In addition, information on the nature of effects exercised by dominants, both alien and native, on large areas of vegetation remains scant and ambiguous (Richardson et al., 1989; Powell et al., 2013; Stohlgren and Rejmánek, 2014; Chase et al., 2015; Rejmánek and Stohlgren, 2015).

This study examines the above issue through the example of 20 sites occupied by synanthropic plant communities in the low-mountain belt of the Western Caucasus with the well-pronounced predominance of alien and native species. We attempted to answer the following questions:

1. Is the relationship between the degree of dominance and the species richness in communities predominated by alien species really stronger (on average) than that in communities predominated by native species?

2. Is the effect of alien dominants on associated species really more selective (on average)? And, accordingly, does it have more significant consequences for large fragments of plant communities (in terms of species pool size) than the effect of native dominants?

3. Are communities with high degrees of dominance of alien species really distinguished by a higher proportion of synanthropic species in their composition than communities with low shares of alien dominants or communities with high degrees of dominance of native species?

MATERIALS AND METHODS

Field Data Collection

The area under investigation is located in the Belaya River basin, Western Caucasus; it stretches from the city of Maykop (190−220 m above sea level) to the village of Guzeripl' (660−680 m above sea level). Twenty sites 40−60 m² in size occupied by synanthropic plant communities were surveyed. On ten sites, the predominance of the following alien species was clearly manifested: *Asclepias syriaca* (2 sites); *Solidago canadensis* (2 sites); and *Ambrosia artemisiifolia*, *Helianthus tuberosus*, *Impatiens glandulifera*, *Paspalum thunbergii*, *Silphium perfoliatum*, and *Xanthium albinum* (1 site each). The other ten sites were dominated

by native species: *Botriochloa ischaemum*, *Calamagrostis epigeios*, *Echium vulgare*, *Equisetum telmateia*, *Melilotus officinalis*, *Rubus caesius*, *Setaria viridis*, *Sisymbrium loeselii*, *Trifolium pratense*, and *T. arvense* (1 site each). The names of vascular plant species are provided in accordance with Zernov (2006). The natural ranges of many alien species (*Helianthus tuberosus*, *Asclepias syriaca*, *Solidago canadensis*, *Ambrosia artemisiifolia*, and *Silphium perfoliatum*) are located in North America; the center of origin of *Xanthium albinum* is South and Central America; for *Impatiens glandulifera*, it is the Himalayas; and for *Paspalum thunbergii*, it is the Far East. The majority of these species (*Impatiens glandulifera*, *Solidago canadensis*, *Ambrosia artemisiifolia*, *Helianthus tuberosus*, and *Xanthium albinum*) are considered invasive (Vinogradova et al., 2009). On the basis of our data, *Asclepias syriaca* can also be attributed to this group of plants within the area under investigation since it occurs in forest glade communities on river terraces, reaching high abundance levels in some locations.

The test sites are located in habitats belonging to different types: (1) abandoned fields and vegetable gardens in the vicinity of the city of Maykop (two sites predominated by *Asclepias syriaca* and sites dominated by *Solidago canadensis*, *Calamagrostis epigeios*, *Melilotus officinalis*, *Echium vulgare*, *Trifolium pratense*, and *T. arvense*) at 200 m above sea level, in the vicinity of the village of Kamennomostsky (one site with *Silphium perfoliatum*) at 370 m above sea level), and in the village of Guzeripl' (two sites predominated by *Helianthus tuberosus* and *Impatiens glandulifera*) at 660 m above sea level; (2) along dirt roads in the vicinity of the city of Maykop (three sites predominated by *Ambrosia artemisiifolia*, *Botriochloa ischaemum*, and *Equisetum telmateia*) at 200−220 m above sea level and near the township of Krasnooktyabrsky (one site with *Sisymbrium loeselii*) at 280 m above sea level; (3) along edges of disturbed forest areas on the Belaya River terrace in the vicinity of the city of Maykop (two sites dominated by *Solidago canadensis* and *Rubus caesius*) at 200 m above sea level; (4) on a forest glade used for horse grazing in the vicinity of the village of Guzeripl' (predominated by *Paspalum thunbergii*) at 680 m above sea level; and (5) on the meander bar of the Belaya River in the vicinity of the city of Maykop (two sites dominated by *Xanthium albinum* and *Setaria viridis*) at 190 m above sea level.

Within each of the selected sites occupied by plant communities, 25−30 sampling plots 0.5 × 0.5 m in size were established. Some of them were established using the regular method in the form of one or two transects (10 plots per transect), while others were in series of 5−15 plots per test site. In the second case, fragments of communities with high and low projective covers of dominants (estimated visually) were selected. On plots with low shares of dominant species, none of the associated species had a clearly manifested advantage over other species. Aboveground biomass samples were collected on each plot. The following parameters were determined for each sample: (1) total weight of fresh aboveground biomass (W), biomass of the dominant species (W_d), and biomass of associated species (W_s); (2) total number of species (S) and number of associated species (S_s); and (3) degree of dominance ($D = W_d/W$). In addition, the total number of species (N) and the total number of associated species (N_s) were determined for each series of samples.

Field Data Analysis

Analysis of the field data involved the following procedures:

1. Using Spearman's rank correlation coefficient, the relationship character (sign) and strength were estimated for the following pairs of parameters: (1) D and S_s, (2) D and W_s, (3) W_s and S_s, and (4) D and S_r, where S_r is the proportion of variation in the S_s variable not explained by the regression equation (either linear or polynomial) produced for S_s and W_s. In other words, S_r is the deviation of actual S_s values from those computed using this equation.

2. On the basis of the produced regression models and computed Pearson correlation coefficient, the character and strength of relationships between D and S_s, D and W_s, W_s and S_s, and D and S_r were estimated for communities dominated by alien species in general and by native species in general. In addition, the average numbers of associated plant species in biomass samples with similar degrees of dominance (less than 0.20, 0.20−0.39, 0.40−0.59, 0.60−0.79, and ≥0.80) of alien and native species were compared. Statistical significance of the difference between mean values of this parameter was assessed using the *F*-test (ANOVA).

3. For each site (series of samples), groups of five samples with minimum shares of the dominant were formed, and for each of these groups, the total biomass of associated species was determined (1); groups of samples with maximum shares of the dominant where the total biomass of associated species was approximately equal to that in groups of samples with minimum shares of the dominant were formed (2); and the total numbers of species in groups of samples with high and low shares of dominants (N_s') and concurrently with approximately equal biomass of associated species were compared (3). The ratio between the detected (N_s') and not detected ($N_s - N_s'$) numbers of species in samples with low shares of the dominant was considered the expected value for samples with high shares of the dominant. Statistical significance of differences between these ratios was assessed using the χ^2 test. In addition, the species composition similarity was estimated for groups of biomass samples with high and low shares of dominants. For this purpose, the Sørensen similarity index was used: $K_s = 2C/(A + B)$, where A and B are the numbers of species in the com-

pared groups of samples and C is the number of shared species identified in both compared groups of samples. The statistical significance of the difference between mean values of this parameter (K_s) computed for sites dominated by alien and native species was assessed using the Mann−Whitney U test;

4. Additionally, biomass samples collected in different parts of the studied communities were combined into four groups, and their species richness and similarity were compared. Two of these groups included samples with the lowest shares of alien and native dominants (50 samples each); the other two groups included samples with the highest shares of alien and native dominants (145 and 121 samples, respectively). The total biomass of associated species was similar in the combined groups of samples with high and low shares of alien dominants, as well as in the combined groups of samples with high and low shares of native dominants.

5. Summary lists of species were produced for the combined groups of samples with high and low shares of native and alien dominants, and for each of them, the proportion of synanthropic (both obligate and facultative) species was determined, as well as proportions of species belonging to other florocoenoelements. The species were subsumed under certain florocoenoelements in accordance with Ivanov (2019). Also, the occurrence frequencies of synanthropic and nonsynanthropic species in groups of samples with different shares of native and alien dominants were compared.

If the relationship between the share of the dominant and the species richness cannot be fully explained by the "energy−diversity" and "larger number of individuals" hypotheses (the number of associated species is a positive function of their biomass, while their biomass is a negative function of dominant's relative abundance), then the relationship between D and S_r can be expected to be significantly negative, and the group of samples with high shares of a certain dominant can be expected to include a significantly smaller number of species than the group of samples with a similar total biomass of associated species and low shares of this dominant. These effects, in turn, can be considered indicators of selective effects exercised by dominants on associated species. Higher proportions of synanthropic species in communities with significant shares of the dominant compared to communities with low shares of the dominant can also indicate this (Hejda and Pyšek, 2006; Hejda et al., 2009; Veselkin and Dubrovin, 2019), as well as a low species similarity between sites with high and low degrees of dominance (Hejda et al., 2009).

Therefore, if alien dominants pose a greater threat to the species richness of plant communities than native ones, then the following patterns can be expected: (1) the relationships between D and S_s and between D and S_r should be stronger on sites predom-

inated by alien species than on sites with native dominants; (2) the situation when a group of samples with high degrees of dominance includes a significantly smaller number of species than a group of samples with a similar total biomass of associated species and low degrees of dominance should be observed more often on sites dominated by alien species than on sites with native dominants; (3) the proportion of synanthropic species in the composition of phytocoenoses with high and low shares of alien dominants should differ to a greater extent compared to communities with high and low degrees of dominance of native species; and (4) on average, the species composition similarity between groups of samples with high and low shares of alien dominants should be lower than the similarity between groups of samples with high and low degrees of dominance of native species.

RESULTS

Data on the shares of dominants and numbers of associated plant species in biomass samples collected on 20 sites occupied by synanthropic vegetation are presented in Table 1. As can be seen, the biomass of alien dominants in the studied parts of communities is on average higher in comparison with native dominants. *Silphium perfoliatum*, *Helianthus tuberosus*, and *Impatiens glandulifera* (i.e., alien species) feature the highest (on average) biomass. The biomass of some native species (e.g., *Echium vulgare*, *Equisetum telmateia*, and *Sisymbrium loeselii*) is also significant, but still lower in comparison with the above alien plants. Table 1 also indicates that the shares of dominants are very high in all the studied communities (at least on some of sampling plots 0.25 m^2 in size): in biomass samples, their shares reach more than 90%. On average, the share of alien dominants in biomass samples is slightly higher in comparison with native dominants. The average numbers of species identified in individual biomass samples collected in communities dominated by alien and native species are approximately the same, as well as the numbers of species in series of samples.

The relationships between D and S_s, D and W_s, W_s and S_s, and D and S_r are provided in Table 2. The following conclusions can be drawn from it: (1) in most communities (dominated both by alien and native species), a moderately or strongly negative relationship between D and S_s is observed; (2) the relationship between D and W_s is strongly or moderately negative; (3) the relationship between W_s and S_s, is strongly, moderately, or weakly positive; and (4) a statistically significant negative relationship between D and S_r is observed only on two sites dominated by native species *Melilotus officinalis* and *Rubus caesius*. On average, the strength of relationships (i.e., values of Spearman's rank correlation coefficient) between all the examined parameters (D and S_s, D and W_s, W_s and S_s, and D and

Table 1. Shares of dominant species and species richness on sites occupied by synanthropic plant communities

Dominant species	n	W_d	D	S	N
Alien					
Helianthus tuberosus	30	961/116/2353	0.62/0.18/0.99	10.2/2/19	37
Asclepias syriaca	30	380/34/1318	0.64/0.09/0.96	6.0/3/10	19
Asclepias syriaca	30	391/26/1026	0.64/0.12/0.94	5.8/3/9	21
Silphium perfoliatum	30	1143/81/2633	0.85/0.19/0.99	10.1/3/24	50
Ambrosia artemisiifolia	25	422/52/862	0.56/0.11/0.95	7.8/5/11	25
Solidago canadensis	25	269/56/455	0.70/0.28/0.98	9.2/4/16	34
Solidago canadensis	25	381/151/582	0.78/0.39/0.99	7.5/4/15	33
Paspalum thunbergii	25	266/107/449	0.71/0.32/0.91	10.3/8/15	26
Impatiens glandulifera	30	800/165/1815	0.70/0.36/0.95	11.4/5/18	29
Xanthium albinum	25	219/63/513	0.81/0.53/0.99	5.4/3/9	37
On average for all sites	275	542.6 ± 30.9	0.70 ± 0.01	8.4 ± 0.23	31.1 ± 2.9
Native					
Botriochloa ischaemum	25	57/9/109	0.47/0.12/0.84	7.4/4/11	32
Trifolium pratense	30	310/11/562	0.57/0.04/0.89	8.3/4/16	27
Melilotus officinalis	30	297/59/576	0.66/0.29/0.97	7.2/3/12	34
Calamagrostis epigeios	30	157/59/278	0.59/0.28/0.93	6.4/3/12	28
Echium vulgare	30	645/24//2174	0.77/0.09/0.99	8.2/5/12	29
Sisymbrium loeselii	30	520/48/1290	0.54/0.09/0.91	16.8/9/24	31
Trifolium arvense	25	239/58/448	0.60/0.18/0.85	7.1/4/11	47
Equisetum telmateia	25	422/23/1337	0.70/0.18/0.94	9.9/6/16	42
Rubus caesius	30	308/38/713	0.60/0.14/0.98	6.9/4/13	28
Setaria viridis	25	57/21/114	0.74/0.45/0.98	4.9/8/9	20
On average for all sites	280	308.8 ± 17.2	0.62 ± 0.01	8.4 ± 0.25	31.8 ± 2.4

n is the number of samples in groups, W_d is the biomass of the dominant species (mean/min/max values), D is the degree of dominance, S is the number of species per 0.25 m^2, and N is the total number of species in sampling series.

S_r) on sites predominated by alien and native species differs statistically insignificantly (the null hypothesis was tested using the nonparametric Mann–Whitney U test).

The relationships between D and S_s, D and W_s, W_s and S_s, and D and S_r in communities predominated by alien species in general and predominated by native species in general are provided in Table 3. As can be seen, the character of these relationships is similar in communities predominated by species of different origin: in both cases, the first three relationships represent relatively weak, but statistically significant correlations; the relationship between D and S_r is nonexistent in both cases. Figure 1 shows relationships between D and S_s and D and S_r. It can be seen that the regression lines in the field of graphs are either located close to each other (Fig. 1a) or coincide (Fig. 1b). As follows from Table 4, the average species richness of samples with similar degrees of dominance of alien and native species differs in most cases statistically insignificantly.

Data on total numbers of associated plant species (N_s') in groups of biomass samples with the highest and lowest shares of dominants (D) are provided in Table 5. Groups with low shares of dominants consist of five samples; groups with high shares consist of 8–21 samples. Importantly, the total biomass of associated species (W_s) is similar in the compared groups of samples. As can be seen in this table, only in five groups of samples with high shares of dominants (alien: *Asclepias syriaca* and *Solidago canadensis*; native: *Trifolium arvense*, *Equisetum telmateia*, and *Rubus caesius*) are the total numbers of species significantly smaller than in groups of samples with low shares of dominants (the difference is significant at $P < 0.05$). Combined groups of biomass samples with relatively low shares of dominants consist of 50 samples (collected on plots whose total area is 12.5 m^2); with relatively high shares, they consist of 145 samples predominated by alien species (collected on 36.25 m^2) and 121 samples with native dominants (collected on 30.25 m^2). As can be seen in this table, the total num-

Table 2. Spearman's rank correlation coefficients computed for the relationships $S_s(D)$, $W_s(D)$, $S_s(W_s)$, and $S_r(D)$

Dominant species	n	Relationships			
		$S_s(D)$	$W_s(D)$	$S_s(W_s)$	$S_r(D)$
Alien					
Helianthus tuberosus	30	−0.654**	−0.772**	0.665**	0.167
Asclepias syriaca	30	−0.567**	−0.904**	0.566**	−0.294
Asclepias syriaca	30	−0.683**	−0.847**	0.620**	−0.060
Silphium perfoliatum	30	−0.893**	−0.950**	0.844**	−0.188
Ambrosia artemisiifolia	25	−0.368	−0.750**	0.410*	−0.073
Solidago canadensis	25	−0.661**	−0.943**	0.714**	−0.080
Solidago canadensis	25	−0.857**	−0.974**	0.894**	0.037
Paspalum thunbergii	25	−0.297	−0.932**	0.270	0.000
Impatiens glandulifera	30	−0.653**	−0.806**	0.362*	−0.357
Xanthium albinum	25	−0.642**	−0.882**	0.759**	−0.025
Native					
Botriochloa ischaemum	25	−0.749**	−0.736**	0.866**	−0.255
Trifolium pratense	30	−0.607**	−0.889**	0.572**	−0.108
Melilotus officinalis	30	−0.648**	−0.746**	0.344	−0.413*
Calamagrostis epigeios	30	−0.698**	−0.874**	0.265	−0.017
Echium vulgare	30	−0.190	−0.928**	0.112	0.020
Sisymbrium loeselii	30	−0.247	−0.820**	0.349	0.120
Trifolium arvense	25	−0.638**	−0.920**	0.670**	−0.039
Equisetum telmateia	25	−0.604**	−0.569**	0.341	−0.366
Rubus caesius	30	−0.630**	−0.624**	0.506**	−0.496**
Setaria viridis	25	−0.647**	−0.901**	0.699**	−0.153

n is the number of biomass samples. * The rank correlation coefficient values are statistically significant at $P < 0.05$. ** The rank correlation coefficient values are statistically significant at $P < 0.01$.

Table 3. Character of the relationships $S_s(D)$, $W_s(D)$, $S_s(W_s)$, and $S_r(D)$ in communities predominated by alien species in general and by native species in general

Relationships	Dominant species					
	alien			native		
	n	model	r	n	model	r
$S_s(D)$	275	$S_s = -7.68D + 13.77$	−0.477**	280	$S_s = -6.23D + 12.25$	−0.347**
$W_s(D)$	275	$W_s = -436.15D + 470.89$	−0.685**	280	$W_s = -319.83D + 325.37$	−0.540**
$S_s(W_s)$	275	$\log S_s = 0.29\log W_s + 1.99$	0.623**	280	$\log S_s = 0.28\log W_s + 2.10$	0.628**
$S_r(D)$	275	$S_r = -0.93D + 1.16$	−0.071	280	$S_r = -1.29D + 1.34$	−0.090

n is the number of biomass samples, and r is the Pearson correlation coefficient. ** r values are statistically significant at $P < 0.01$.

bers of plant species in the compared groups of samples (N_s') differ statistically insignificantly.

On average for ten plots, the species composition similarity (K_s) between groups of samples with high and low shares of certain alien dominants is 0.69 ± 0.04; between groups of samples with high and low shares of certain native dominants, it is 0.63 ± 0.03. The difference between these values is not statistically significant (Mann–Whitney U test, $U = 37$). The lowest species composition similarity was identified between groups of samples with high and low shares of native dominants *Melilotus officinalis*, *Trifolium arvense*, and *Rubus caesius* (0.50–0.55). The species
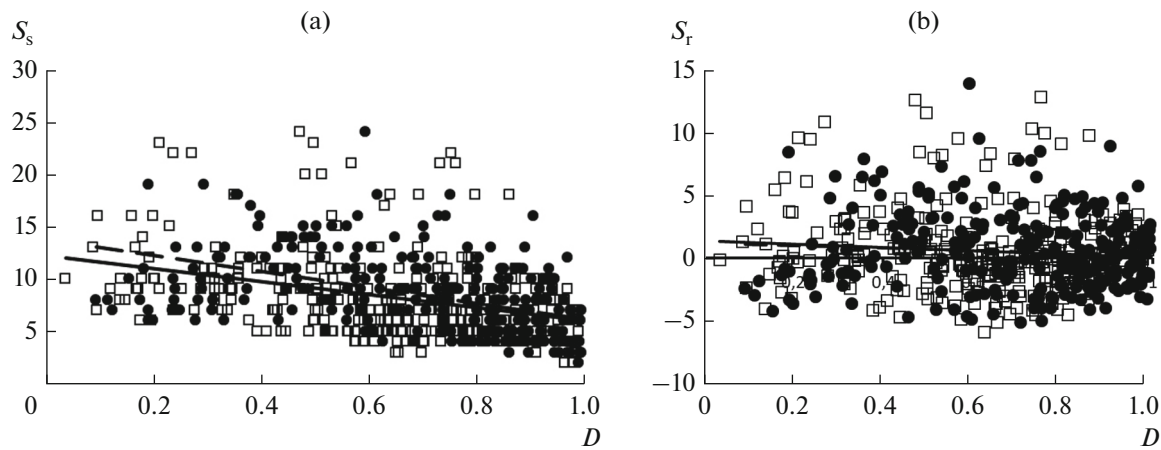
Fig. 1. $S_s(D)$ and $S_r(D)$ ratios in communities predominated by alien species in general and predominated by native species in general. Black circles and dashed regression lines represent biomass samples with the predomination of alien species; white circles and solid regression lines represent biomass samples with the predomination of native species.

composition similarity (K_s) between combined groups of samples with high and low shares of alien dominants is 0.80; between combined groups of samples with high and low shares of native dominants, it is 0.76.

Figure 2 shows that the occurrence frequency of associated plant species in combined groups of samples with high shares of alien and native dominants is mostly lower than in groups of samples with their low shares. In addition, it was determined that the proportion of synanthropic species (both obligate and facultative ones) that feature a higher occurrence frequency in the combined group of samples with low shares of native dominants than in the group of samples with their high shares is 0.81; the share of nonsynanthropic species is 0.77 (the difference is not statistically significant: $t = 0.57$, $P < 0.05$). For groups of samples predominated by alien species, the values of these parameters are 0.86 and 0.88, respectively (the difference is also statistically insignificant: $t = 0.32$, $P < 0.05$). Table 6 shows the distribution of species identified in

groups of biomass samples with low and high shares of native and alien dominants by florocoenoelements. It follows from this table that, in communities dominated by alien species, the proportion of synanthropic (ruderal) plant species is somewhat lower, while the proportion of meadow species is somewhat higher than in communities with native dominants (on sites with both their low and high shares).

DISCUSSION

Overall, alien dominants feature significantly higher aboveground biomass values and somewhat higher degrees of dominance in the studied synanthropic communities than native dominants. Having said that: (1) the average numbers of species on sites 0.25 m² in size with high shares of alien and native dominants are roughly the same; (2) on average, the relationship between the degree of dominance of alien species and the species richness is approximately as

Table 4. Average species richness of plant communities on plots 0.25 m² in size with different degrees of dominance of alien and native species

Parameters	Degree of dominance (D)				
	<0.20	0.20–0.39	0.40–0.59	0.60–0.79	≥0.80
Alien dominants					
n	10	30	48	66	121
S	9.0 ± 1.2	11.2 ± 0.7	10.9 ± 0.5	8.9 ± 0.4	6.4 ± 0.2
Native dominants					
n	16	29	56	101	73
S	10.6 ± 0.8	10.8 ± 0.8	9.3 ± 0.6	7.8 ± 0.4	6.5 ± 0.3
F	1.45	0.15	4.08*	3.11	0.07

F is Fisher's F-test (ANOVA). * The actual F value is higher than the critical one at $P < 0.05$.

Table 5. Total numbers of associated plant species in groups of samples with low and high shares of dominants

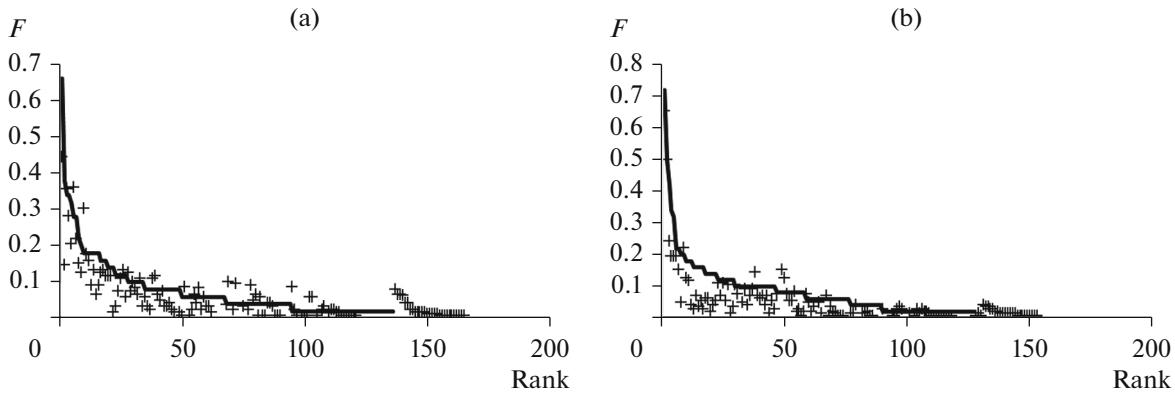| Dominant species	N_s	Low shares of dominant					High shares of dominant				
		n	D	W_s	S_s	N_s'	n	D	W_s	S_s	N_s'
Alien											
Helianthus tuberosus	37	5	0.24	2598	11.8	21	15	0.9	2607	6.3	23
Asclepias syriaca	19	5	0.2	1024	5.8	11	13	0.87	1020	4.2	10
Asclepias syriaca	21	5	0.2	1268	6.6	15	14	0.86	1268	4	10*
Silphium perfoliatum	50	5	0.47	1329	17.4	37	21	0.95	1330	6.6	31
Ambrosia artemisiifolia	25	5	0.23	2560	8	16	11	0.72	2546	5.9	16
Solidago canadensis	34	5	0.38	858	14.4	28	14	0.85	856	6.9	22**
Solidago canadensis	33	5	0.46	1042	11.4	24	18	0.87	1042	6.1	25
Xanthium albinum	26	5	0.58	451	6.2	16	16	0.9	455	3.8	18
Paspalum thunbergii	29	5	0.5	998	9.6	17	13	0.79	996	8.6	21
Impatiens glandulifera	37	5	0.42	1704	14.2	24	10	0.88	1701	7.6	26
Total	150	50	0.40	13831	10.8	121	145	0.86	13833	6.5	117
Native											
Botriochloa ischaemum	32	5	0.24	479.8	9.2	21	11	0.64	478.6	5.4	17
Trifolium pratense	27	5	0.15	1527.2	10.8	17	12	0.78	1527.6	7.3	17
Melilotus officinalis	34	5	0.37	902.6	9.2	21	11	0.84	902.2	6.1	21
Calamagrostis epigeios	28	5	0.38	880.8	8	23	13	0.74	887.4	6.1	21
Echium vulgare	29	5	0.15	994	7.6	19	16	0.93	994	7.1	26
Trifolium arvense	31	5	0.27	1231	8.8	21	12	0.75	1228	4.9	15*
Sisymbrium loeselii	47	5	0.15	3413	15.2	32	13	0.74	3404	15.6	38
Equisetum telmateia	42	5	0.38	772	12.6	32	8	0.87	777	7.5	24*
Rubus caesius	27	5	0.23	427.8	10.0	20	10	0.78	427.2	5.5	9**
Setaria viridis	20	5	0.51	48.3	6.4	14	15	0.83	48.4	4.3	15
Total	163	50	0.28	11827	10.8	130	121	0.78	11826	7.3	126

n is the number of samples in groups, D is the average degree of dominance per sample, W_s is total biomass of associated species in groups of samples, S_s is the average number of associated species per sample, N_s is the total number of associated species in series of samples, and N_s' is the number of associated species identified in groups of samples with different shares of the dominant. * N_s' to $(N_s - N_s')$ ratio in groups of samples with high shares of the dominant is statistically significantly lower than in groups of samples with its low shares at $P < 0.05$ (χ^2 test). ** N_s' to $(N_s - N_s')$ ratio in groups of samples with high shares of the dominant is statistically significantly lower than in groups of samples with its low shares at $P < 0.01$ (χ^2 test).

Table 6. Distribution of species identified in groups of biomass samples with low and high shares of native and alien dominants by florocoenoelements

Dominants	Native		Alien	
Average degree of dominance	0.28	0.78	0.40	0.86
Number of species	50	121	50	145
Total number of species in biomass samples	130	126	121	117
Obligatory ruderal (R)	0.24	0.24	0.19	0.18
Facultative ruderal (RP, RS, RA)	0.23	0.21	0.17	0.16
Forest (S)	0.14	0.14	0.09	0.12
Forest-meadow (SP)	0.01	0.02	0.07	0.06
Meadow (P)	0.24	0.25	0.32	0.33
Steppe (ST)	0.12	0.10	0.09	0.09
Aqual (A)	0.03	0.04	0.07	0.06

The table show proportions of species belonging to certain florocoenoelements in the total number of species (the species were subsumed under certain florocoenoelements in accordance with Ivanov (2019)).

Fig. 2. Occurrence frequency of associated plant species (*F*) in combined groups of samples with high and low shares of native (a) and alien (b) dominants. The *x* axis shows occurrence frequency (*F*) ranks of species in biomass samples with low shares of dominants. Solid lines show *F* values of species in samples with low shares of dominants; crosses show *F* values of the same species in samples with high shares of dominants.

strong as the relationship between the degree of dominance of native species and the species richness; and (3) the "energy–diversity" and "larger number of individuals" hypotheses satisfactorily explain the relationship between these parameters both for individual sites and in general for all biomass samples with the predomination of alien or native species. Exceptions are two fragments of communities predominated by native species (*Melilotus officinalis* and *Rubus caesius*).

In addition, the total number of species identified in combined groups of biomass samples with high shares of both native and alien species turned out to be approximately the same as in groups of samples similar in total biomass but with low dominance levels of native and alien species. With regard to fragments of communities predominated by certain species, only five of them in groups of samples with relatively high shares of dominants (in two cases with the predominance of alien species and in three cases with the predominance of native ones) feature significantly smaller numbers of species in comparison with groups of samples with similar biomass reserves of associated species and low shares of dominants. It must also be noted that *Asclepias syriaca* and *Solidago canadensis* were studied on two sites each, and the results obtained on these sites turned out to be different. This may be due to random processes or due to the fact that the impact of the same dominants may have different consequences in different communities (Hejda et al., 2017; Vítková et al., 2017).

Finally, our data indicate that the occurrence frequency of most associated species decreases as shares of both native and alien dominants go up. Furthermore, in both cases, occurrence frequencies of synanthropic and nonsynanthropic species decrease to the same extent. Therefore, the proportion of synanthropic species in communities with high shares of both alien and native dominants is not higher than in communities with their low shares. In addition, the

species composition similarity between groups of samples with high and low shares of alien dominants turns out to be approximately the same as between groups of samples with high and low shares of native dominants.

Overall, the results obtained by applying different methods of analysis to the field data are generally in good agreement with each other and indicate a similar and predominantly nonselective nature of impacts exercised by alien and native dominants on associated species in plant communities. Accordingly, we found no evidence that alien dominants pose a greater threat to the species richness of plant communities than native ones. According to our data, the only species exercising a selective effect on other species is *Rubus caesius* that predominates the edge community. This is a native low-growing perennial shrub whose shoots crawl and take roots forming a dense canopy. Apparently, an increase in its canopy density leads to the disappearance of species sensitive to low-light conditions, including *Convolvulus arvensis*, *Achillea millefolium*, *Vicia pannonica*, *V. hirsuta*, *Plantago lanceolata*, *Inula germanica*, and *Torilis arvensis*. *Poa pratensis*, *Elytrigia repens*, *Calystegia silvatica*, *Stellaria holostea*, and some other species persist in areas with high proportions of dewberry biomass and, accordingly, with high canopy density levels. Of them, *Calystegia silvatica* and *Stellaria holostea* occur in forests and shrub thickets, while *Elytrigia repens* often predominates in edge phytocoenoses in the area under investigation. There are three possible reasons why this shrub exercises a more selective effect on associated plant species compared to herbaceous species: (1) there is a predominantly horizontal arrangement of its leaves; (2) the dense canopy formed by *Rubus caesius* above the grass stand can mechanically prevent the upward growth of grasses; and (3) compared to wasteland and fallow communities, edge communities include species that are more differentiated in terms of shade tolerance.

According to Hejda et al. (2009), species forming tall and dense thickets unsuitable for the growth of shade-sensitive plants have the strongest effect on accompanying species in herbaceous cenoses. Overviews included in *Black Book of the Flora of Central Russia* (Vinogradova et al., 2009) also indicate this. Gioria and Osborne (2014), as well as Czarniecka-Wiera et al. (2019), note that the shading effect exercised by alien species owing to their significant biomass is one of the main mechanisms of impact affecting recipient communities. Therefore, taking that biomass of alien dominants on the studied sites is, on average, greater than biomass of native dominants, one could expect the consequences of their impacts on synanthropic communities to be different. In this regard, it must be noted that our results do not necessarily indicate the complete absence of differences between impacts exercised by alien and native dominants. But it follows from our data that the role of these differences in the formation of the studied communities is, apparently, relatively small compared to other environmental processes (fluctuations in the abiotic environment, disturbances, inflow of propagules, etc.).

Our findings are not unexpected: similar conclusions were made by other authors as well. For instance, Houlahan and Findlay (2004) showed that the share of alien dominants exercising significant adverse impacts on local plant communities in 58 inland wetlands in Ontario (North America) is the same as the share of native dominants exercising similar effects. Hejda et al. (2021) examined the impacts of several native and alien dominants on plant communities in Central Europe and did not find significant differences between them in this respect. Powell et al. (2013) compared sites occupied by forest biomes of different types (Hawaii, Missouri, and Florida, USA) dominated by alien tree species with forest sites featuring similar growing conditions but dominated by native plants present in smaller proportions. The results indicate that communities dominated by alien species feature lower species richness than similar communities with native dominants on small sites; however, on large sites, communities dominated by species of different origins feature similar species richness values. Similar results were obtained for plant communities on abandoned pastures in Poland (Czarniecka-Wiera et al., 2019). A number of overviews also note that the increasing number and abundance of alien plant species do not cause significant consequences for the phytodiversity of recipient regions (Gaertner et al., 2009; Powell et al., 2011; Rejmánek et al., 2013).

However, it must be noted again that other data indicate a stronger impact of alien species on communities compared to native ones and/or the selective nature of this impact (Richardson et al., 1989; Standish et al., 2001; Hejda et al., 2009; Akatov et al., 2012; Gusev, 2016, 2017; Rijal et al., 2017; Veselkin et al., 2020; etc.). In addition, two circumstances must be taken into account; in our opinion, they may be the reasons behind some underestimation of consequences caused by the impact of dominants (both alien and native ones) on other species. The first circumstance applies both to our findings and to results obtained by other authors: in most cases, the impact of dominant species on the species richness of plant communities is estimated on different spatial scales based on data collected on their relatively large fragments (Richardson et al., 1989; Hejda et al., 2009; Powell et al., 2011, 2013; Stohlgren and Rejmánek, 2014; Rejmánek and Stohlgren, 2015). However, within such relatively large fragments of communities with a high (on average) projective cover of dominants, microsites with a relatively low projective cover of dominants ("openings") can be distinguished, which can affect the results of the dominance effect assessment (Hejda and Pyšek, 2006). This is why this study uses data collected on series of homogeneous microplots (0.25 m^2) established using both the regular and typical methods within larger fragments of phytocoenoses dominated by certain species. In addition, purposeful sampling was used to enhance the contrast between samples in terms of shares of dominants. But even in such cases, the formed groups of biomass samples with high (on average) shares of dominant species often include samples with moderate degrees of dominance that could include species sensitive to the impact of this factor.

The second circumstance pertains to the mechanism that, according to the "larger number of individuals" hypothesis, determines the relationship between the productivity and species richness in communities: productivity limits the density of individuals, while the density of individuals limits the number of species. A key link in this causal chain is the density of individuals. However, the number of individuals on small sites depends not only on the aboveground biomass but also on their size, which presumably can decrease along the growth gradient of the share of the dominant. Therefore, the number of individuals and, accordingly, species in biomass samples with significant shares of dominants may in some cases be somewhat higher than one could expect according to the biomass weight.

CONCLUSIONS

Overall, our results support the assumption that, on average, alien and native dominants exercise similar impacts on synanthropic plant communities, and an increase in their share leads to a nonselective (i.e., random) elimination of associated species from communities. Such impacts cannot significantly affect the species pool size in phytocoenoses and, accordingly, the species richness of large fragments of vegetation cover. Nevertheless, in communities with high shares of dominants, the occurrence frequency of most associated species is lower than in communities with low

shares of dominants. This makes such communities more vulnerable to impacts of other factors (e.g., phytophagous organisms, environmental fluctuations, fragmentation, etc.). But since the nature of such impacts weakly depends on the origin of dominants, the replacement of native dominants in the vegetation cover by alien ones should not cause significant consequences for accompanying species, at least, on large sites.

It must be noted though that, for a number of reasons, the ongoing increase in the total area of fragments of vegetation cover dominated by herbaceous alien species cannot be considered absolutely harmless for the phytodiversity of recipient regions. First, in some cases, alien dominants can reach significantly higher abundance levels than local dominants. Second, it is known that grass communities, including synanthropic ones, often do not have well-defined dominants. For instance, within the area under investigation, such communities occupy some 40% of lands covered by ruderal vegetation. The penetration of alien species into communities having no well-defined dominants and the subsequent growth of their shares are likely to cause more significant consequences for the species richness of recipient communities than strengthening of the positions of alien dominants in initially monodominant cenoses. Third, the available data indicate that alien dominants can stop restorative successions at the stage of monodominant communities poor in species for a long period of time (Gusev, 2016, 2017). Finally, most researchers assess the consequences of impacts exercised by alien dominants on communities in relation to associated plant species. But local dominants may be more vulnerable to such impacts. The ideas of Mirkin and Naumova (2012) on the organization of herbaceous phytocoenoses support this supposition. In their opinion, herbaceous phytocoenoses are structured by different mechanisms: competition between dominants (C-strategists) and random processes in groups of less abundant species (S- and R-strategists). However, we are not aware of studies examining the relationships between dominants of different origins in herbaceous communities on a large spatial scale.

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