Factors of Variation in the Number of Adventive Species in Herbaceous Communities of the Western Caucasus

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Abstract—The saturation of herbaceous communities with adventive species in the Northern Caucasus has been estimated using as an indicator the number of such species in 0.5-m^2 plots. Among factors accounting for variation in the test parameter, consideration has been given to the coverage of the herbaceous layer, the species richness of communities (in 0.5-m^2 plots), and the numbers of adventive and indigenous species (in 15-m^2 plots). The field data have been processes by methods of ordinary and multivariate regression analysis. The results show that variation in saturation with adventive species between small areas of herbaceous communities largely depends on the number of such species in larger areas, their species-holding capacity, and the level of completeness of communities.

Key words: adventive species, herbaceous communities, species-holding capacity, species completeness, coverage, the Western Caucasus.

Adventization of vegetation may have serious consequences not only for plant species native to corresponding regions but also for the health and welfare of their residents (Davis et al., 2000; Mirkin and Naumova, 2002; Shvarts, 2004). Therefore, the question as to why some communities are saturated with adventive species to a higher degree than others is of both scientific and practical interest and has been actively discussed by ecologists in recent years (Mirkin and Naumova, 2002; Réjmánek et al., 2005; Richardson and Pysek, 2006). Studies in this field will hopefully provide a deeper insight into the mechanisms of community resistance to invasion by such species, thereby allowing more objective prognosis of the expectable magnitude and hazard of this process.

In this respect, the most popular and debatable idea in this respect is provided by Elton (1958) in his diversity–invasibility hypothesis, according to which the higher the species diversity of cenoses (and, therefore, the degree of resource utilization and the level of interspecific competition), the lower the probability of their invasion by adventive species. However, the results of testing this hypothesis are ambiguous. In particular, they show that resource utilization may be incomplete in species-rich as well as in species-poor cenoses (Moore et al., 2001) and that the strength and direction (sign) of correlation between the number of adventive species and the species richness of communities largely depend on the type of community (Davies et al., 2007; Vila et al., 2007) and its spatial extent (Brown and Peet, 2003; Fridley et al., 2004; Herben et al., 2004; Réjmánek et al., 2005). Thus, the above correlation may indeed be negative in small areas of up to 1 m^2 (which is not always the case; Davies et al., 2007), but its sign usually changes to positive as the test area increases. In general, however, environmental factors providing for a high species-holding capacity of communities are often also favorable for adventive species (Sax and Brown, 2000; Brown and Peet, 2003; Gilbert and Lechowicz, 2005; Richardson and Pysek, 2006; Davies et al., 2007).

Numerous observations also show that the greatest numbers of adventive species usually grow in periodically disturbed open communities (segetal, ruderal, communities on fallow lands, roadsides, river shoals, etc.), which represent the initial stages of primary or secondary succession (Mirkin and Naumova, 2002; Réjmánek et al., 2005). This may be due to availability of unutilized resources (Davis et al., 2000; 2005) or a low level of interspecific competition in such communities (Mirkin and Naumova, 2002).

Rabotnov (1983) considers that the invasion of new species into plant communities may be facilitated by their species incompleteness resulting from isolation of these communities or the poverty of their species pools. Evidence in favor of this viewpoint is found in data on a high degree of adventization in insular floras (Sax, Brown, 2000; Mirkin and Naumova, 2002;

Sax et al., 2005) and on numerous cases of invasions not accompanied by the loss of native species (Ricklefs and Schluter, 1993; Sax and Gaines, 2003; Sax et al., 2005). There is also the opinion that a high level of adventization in segetal communities may be explained by their young evolutionary age and, therefore, by incompleteness of their species pools (Sax and Brown, 2000; Zherikhin, 2003).

Finally, we cannot but mention the opinion that the degree of saturation with adventive species in local areas of plant communities depends on the number of such species that can grow in the corresponding region under certain conditions and supply these areas with their diaspores (Usher et al., 1988; Lonsdale, 1999; Meekins and McCarthy, 2001; Hierro et al., 2005; Richardson and Pysek, 2006). If this opinion is correct, then a higher degree of adventization in certain communities, compared to others, does not necessarily indicate their higher intrinsic invasibility (Richardson and Pysek, 2006). In particular, explerent species have stronger capacities for transcontinental seed dispersal and, hence, play a leading role in plant cover adventization in new regions. Since most of these species in their native growing regions are involved in the initial stages of progressive succession, they mainly invade frequently disturbed phytocenoses (Baker, 1965; cited from Réjmánek, 1989; Réjmánek et al., 2005). Therefore, a relatively higher degree of adventization in such communities may well be due not to their great invasibility but rather to an increased number of adventive species in their species pools.

The majority of publications on the problem at issue deal with only one of many factors potentially capable of influencing community saturation with adventive species (Davis et al., 2000; Brown and Peet, 2003; Fridley et al., 2004; Herben et al., 2004; Akatov and Akatova, 2008; etc.). We made an attempt to consider the combined effect of several factors on the number of adventive species in herbaceous communities of the Western Caucasus and to estimate the relative role of each factor, performing analysis both at the level of individual communities and at the intercenotic level.

MATERIAL AND METHODS

Field data were collected in the basins of the rivers Belaya, Kisha, Malaya Laba, Shepsi, Pszeuapse, and Western Dagomys (the Western Caucasus) in different plant communities. They included open communities (groups) on shoals along low-mountain river courses on the southern (the Shepsi, Pszeuapse, Western Dagomys) and northern macroslopes (the Belaya) and along mid-mountain sections of the Malaya Laba and Belaya rivers; communities of mid-mountain forest glades and low-mountain steppificated meadows used for hay harvesting or livestock grazing; and communities of annual crop fields (wheat, corn, sunflower, and soybean) and fallow lands (the Belaya River basin).

Releves of communities were made in 15-m^2 plots, each with 20 small plots (0.5 m^2) arranged in a regular pattern. In both large and small plots, we recorded all herbaceous species and visually estimated their total coverage (in fractions rounded off to the nearest five-hundredths: 0.05, 0.10, 0.15, 0.20, etc.). The plots were established so as to describe areas with different numbers of adventive species within each type of communities. On the whole, releves of 128 large plots with adventive species were described, including 38 plots on river shoals within the low-mountain belt, 26 plots on river shoals of the mid-mountain belt, 16 plots in glades and steppificated meadows, 25 plots in crop fields, and 23 plots in fallow lands. The distances between the plots described on shoals in the low-mountain section of the Belaya River and between the plots in steppificated meadows did not exceed 0.5 and 5 km, respectively; in all other communities, the plots were located more than 20 km apart from each other.

The releves were used to determine the following parameters: S, the average number of all plant species per 0.5-m^2 plot; S_a, the average number of adventive species per 0.5-m^2 plot; N_a and N_n, the numbers of adventive and native species per 15-m^2 plot; Cov, overall plant coverage in large plots; and P_a, the total number of adventive species recorded in all plots established in communities of a certain type.

The number of adventive species in 0.5-m^2 plots (S_a) was used as an index of community saturation with such species. Their number in large plots (15 m^2) was regarded as the parameter characterizing the actual pool of adventive species (the actual species pool is understood as the number of species growing within the boundary of a community and supplying their diaspores to its different areas; Partel et al., 1996; Zobel et al., 1998). The sizes of the small and large plots were chosen on the premise that the effect of species richness on the number of adventive species can be assessed more accurately in plots smaller than 1 m^2 (Levine, 2000; Brown and Peet, 2003; Réjmánek et al., 2005; Davies et al., 2007), and the size of the actual species pool should be estimated in the largest possible plots, with environmental conditions and vegetation within their boundaries being uniform. Relatively small plots (15 m^2) in our case were used by necessity, with regard to spatial heterogeneity of plant communities on river shoals and fragmentary pattern of steppificated meadows remaining in the study region (small areas along steep riverbanks, between crop fields or forest strips, etc.).

RESULTS AND DISCUSSION

Tables 1 and 2 show data on the composition and species richness of the communities studied, the distribution of adventive species, and their numbers on plots of different sizes. On the whole, 22 adventive species were listed in the releves. Among them, 18 species (over 80%) originated from the American continent,

Table 1. General characteristics of Western Caucasus herbaceous communities used as objects of analysis

Communities	1	2	3	4	5	6	7
Elevation a.s.l., m	70−200	200	440−900	180−220	180−220	200	600−680
Coverage (average and extreme values), %	9 (5−15)	8 (5−15)	12 (5−25)	80 (40−100)	90 (70−100)	85 (50−100)	97 (85−100)
Number of releves	23	15	26	25	23	9	7
Adventive species							
Ambrosia artemisiifolia L.	V (32)	V (25)	II (37)	V (88)	V (43)	III (31)	I (10)
Erigeron annuus (L.) Pers.	I (25)	II (7)	IV (13)	III (48)	V (77)	V (51)	V (70)
Erigeron canadensis L.	II (12)	IV (38)	V (63)	II (23)	II (24)	I (20)	I (25)
Bidens frondosa L.	II (28)	III (20)	I (5)	I (5)	I (30)		
Xanthium californicum Greene	I (15)	III (7)		I (15)	II (14)		
Amaranthus retroflexus L.	I (10)	I (5)		I (15)			
Robinia pseudoacacia L.	I (10)			I (25)			
Oxalis stricta L.				I (19)	III (29)	III (34)	III (62)
Asclepias syriaca L.				I (43)	III (76)	I (5)	
Euphorbia nutans Lagasca	II (18)						
Scrophularia peregrina L.	I (15)						
Amorpha fruticosa L.		I (5)					
Oenothera biennis L.		II (9)	II (41)				
Galinsoga parviflora Cav.		I (5)		I (5)			
Matricaria suaveolens (Pursh) Buchenau				III (34)			
Helianthus annuus L.				III (35)			
Helianthus tuberosus L.				I (10)			
Acalypha australis L.				I (38)			
Sorghum halepense (L.) Pers.				I (10)	I (70)		
Solidago canadensis L.				I (5)	II (100)		
Morus nigra L.					I (30)		
Secale cereale L.					I (5)		
Native species							
Prunella vulgaris L.	II (12)	I (5)	IV (17)	I (10)	II (60)		V (48)
Convolvulus arvensis L.	II (13)	II (14)		V (18)	V (56)	IV (43)	III (55)
Plantago major L.	II (12)	I (10)	II (8)	II (13)	II (46)		III (35)
Polygonum persicaria L.	III (45)	III (59)	I (25)	II (14)	I (10)		
Petasites albus (L.) Gaertner	IV (50)		I (20)				
Setaria viridis (L.) P.Beauv.	IV (57)	V (58)	I (57)				
Echinochloa crus-galli (L.) P. Beauv.	I (15)	III (69)			I (40)		
Chenopodium album L.		III (19)	I (15)	I (10)	I (55)		
Crepis setosa Hall. fil.	I (11)	III (24)	I (10)		I (50)		
Calamagrostis pseudophragmites (Hall. fil.) Koel.		I (5)	V (46)			I (15)	I (10)
Tussilago farfara L.	II (14)	I (5)	IV (15)				
Salix elbursensis Boiss.			IV (47)				
Chenopodium polyspermum L.				III (39)			
Cynodon dactylon (L.) Pers.				V (76)	I (50)		I (10)
Polygonum minus Hudson				IV (30)			
Festuca pratensis Hudson				I (28)	V (81)		II (40)
Potentilla reptans L.	I (43)				IV (27)		
Trifolium medium L.					III (41)	I (10)	
Festuca ovina L.						V (100)	
Centaurea micrantha S.G. Gmelin						IV (54)	
Chondrilla juncea L.						IV (33)	
Agrostis stolonifera L.			II (21)				V (93)
Potentilla erecta L.							V (54)
Salvia verticillata L.							V (33)

Note: Roman numerals are grades of species constancy; Arabic numerals show average frequencies of species occurrence (%) in 0.5-m² plots within a 15-m² plot. All adventive species recorded in the releves and some native species (widespread or characteristic of certain communities) are presented in the table. Here and in Table 2, designations of communities (1−7) are as follows: (1) communities on shoals along low-mountain sections of the Shepsi, Psezuapse, and Western Dagomys rivers; (2) communities on shoals along the low-mountain section of the Belaya River; (3) communities on shoals along mid-mountain sections of the Belaya and Malaya Laba rivers; (4) communities of annual crop fields; (5) communities on fallow lands; (6) communities of steppificated meadows; and (7) communities of mid-mountain forest glades.

Table 2. Species richness and saturation with adventive species of Western Caucasus herbaceous communities used as objects of analysis

Parameter	Community						
	1	2	3	4	5	6	7
N_n	18.0 (8−27)	10.1 (7−14)	18.7 (12−27)	16.4 (10−29)	24.4 (17−39)	20.6 (17−26)	37.3 (20−45)
S	4.8 (2.1−8.4)	3.8 (2.5−5.3)	4.9 (3.0−8.5)	7.9 (4.5−12.8)	11.2 (5.1−17.7)	10.8 (4.9−16.0)	15.3 (6.9−19.5)
S/N_n	0.27 (0.19−0.44)	0.41 (0.25−0.48)	0.26 (0.19−0.41)	0.50 (0.38−0.65)	0.45 (0.28−0.67)	0.51 (0.35−0.66)	0.41 (0.34−0.51)
P_a	9	9	5	16	11	5	4
N_a	2.8 (1−7)	3.9 (2−6)	2.2 (1−4)	3.9 (1−8)	3.3 (1−5)	2.1 (1−4)	1.9 (1−3)
S_a	0.5 (0.1−2.3)	0.7 (0.3−1.3)	0.9 (0.2−3.1)	1.9 (0.1−3.4)	1.9 (1.0−3.4)	0.8 (0.1−2.6)	1.0 (0.3−2.3)
S_a/S	0.1 (0.01−0.33)	0.20 (0.06−0.32)	0.18 (0.04−0.44)	0.24 (0.03−0.48)	0.18 (0.09−0.33)	0.07 (0.01−0.17)	0.06 (0.01−0.10)

the remaining four being natives of eastern Asia, Asia Minor, and the Mediterranean. Over half of the species (55%) were characteristic of the first stages of progressive succession, and others were feral agricultural, industrial, or ornamental plants that escaped from cultivation.

The total numbers of adventive species per large plot were the greatest in communities of crop fields and fallow lands (P_a = 16 and 11, respectively), being slightly smaller in communities on shoals along low-mountain river sections on the northern and southern macroslopes of the Western Caucasus (P_a = 9) and decreasing to a minimum (P_a = 4−5) in communities on shoals along mid-mountain river sections and in steppificated meadows and glades. The distribution of adventive species by different community types in large plots was similar. The number of adventive species per small plot (S_a) and their proportion of the total species number (S_a/S) were the greatest in segetal cenoses; the smallest number of such species was recorded in plant groups on shoals along low-mountain river sections, and their proportion (relative to the total species number) decreased to a minimum in communities of steppificated meadows and glades (Table 2).

The factual material obtained in this study can provide arguments for or against the hypotheses considered above and, therefore, allow us to determine factors responsible for variation in the number of adventive species in herbaceous phytocenoses of the Western Caucasus. Thus, the correlation between parameters S and S_a may be negative, giving evidence for Elton's diversity−invasibility hypothesis, or positive, confirming the thesis that environmental conditions providing for a high species-holding capacity of communities are also favorable for adventive species. If disturbances of plant communities indeed facilitate invasion, a nega-

tive correlation can be expected between the coverage of the herbaceous layer (Cov) and the numbers of adventive species in local community areas.

The ratio between the numbers of native species growing in large and small plots (S/N_n) may be regarded as a parameter characterizing the initial level of the species completeness of communities (before their invasion by adventive plants) (Akatov et al., 2002, 2005; Akatov and Akatova, 2008). Under conditions of increasing species pool, the species richness of communities in small plots is supposed to reach its upper limit (full species-holding capacity) more rapidly than in larger plots (Terborgh and Faaborg, 1980; Akatov et al., 2005; He et al., 2005); hence, the correspondence between the number of species and the holding capacity of the environment is always better in small than in large (Akatov et al., 2002, 2005). Therefore, communities equal in species-holding capacity but differing in the initial level of completeness should be characterized by similar S values but different N_n values: the greater the N_n value (the lower the S/N_n ratio), the higher the level of species completeness. Thus, if the species completeness of the community has an effect on the number of adventive species in 0.5-m^2 plots (S_a), then it can be expected that the values of this parameter will positively correlate with S/N_n.

If the hypothesis is valid that the size of the pool of adventive species has an effect on their numbers in local areas of communities, it follows that a significant positive correlation between N_a and S_a can be expected. It should be taken into account, however, that the existence of such a correlation can be regarded only as evidence (but not proof) for the above hypothesis, because this correlation may be due to the dependence of either N_a or S_a on the third variable (e.g., environmental conditions). On the other hand, the absence of correlation between N_a and S_a may indicate
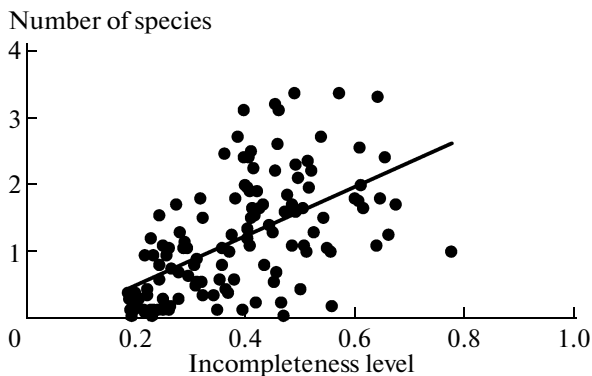
Table 3. Factors accounting for the number of adventive species in local 0.5-m^2 areas of communities (S_a)

Communities	n	Factors	R	R^2	Beta
All habitats	128	Cov	0.764***	0.583	0.239**
		N_n			−0.298**
		S			0.516***
		N_a			0.468***
River shoals	64	Cov	0.713***	0.508	−0.057
		N_n			−0.513***
		S			0.937***
		N_a			0.051
Annual crop fields	25	Cov	0.716**	0.513	0.287
		N_n			−0.315
		S			0.281
		N_a			0.589**
Fallow lands	23	Cov	0.811***	0.657	−0.262
		N_n			−0.072
		S			0.413
		N_a			0.667***
Glades and steppificated meadows	16	Cov	0.840**	0.705	0.110
		N_n			−0.285
		S			0.618*
		N_a			0.627**

Note: (n) the number of releves, (R) multiple correlation coefficient, (R^2) multiple determination coefficient, (β) standard regression coeffi-
cient for comparing relative contributions of each independent variable (factor) to prediction of dependent variable; significance levels:
* $p < 0.1$, ** $p < 0.01$, *** $p < 0.001$.

that the number of adventive species in small areas of communities depends not on the size of their pool but on certain intrinsic factors (biotic or abiotic) that hamper or facilitate their establishment in these areas.

The corresponding factual material was processed by methods of ordinary and multivariate regression analysis. The latter method makes it possible to esti-

Number of species

Relationship between the level of species incompleteness (S/N_n) and the number of adventive plant species in 0.5-m^2 plots (S_a) in herbaceous communities of the Western Caucasus.

mate the total contribution of several factors to the variance of dependent variable as well as the relative effect of each factor on this variable, regardless of the relationship between variation in this and other factors (Eliseeva and Yuzbashev, 1996). The relative contribution of each factor to prediction of S_a was estimated using the standard regression coefficient (β). The type and strength of relationships between S_a and certain factors were additionally evaluated with Pearson's pairwise correlation coefficient. Calculations were made using the Microsoft Excel and Statistica programs.

The results of this analysis (Table 3) show that factors Cov, N_n, S, and N_a have a significant combined effect on the number of adventive species in small plots (S_a) and jointly account for almost 60% of its variance in the whole data set. Their joint contribution to the variance of S_a in individual types of communities is also significant, exceeding 70% in meadows and glades, 60% on fallows, and 50% on river shoals and in crop fields. However, individual factors differently contribute to the variance in the degree of community saturation with adventive species.

Noteworthy is the significant positive correlation between S_a and the number of adventive species in large plots (N_a), which is observed both in the whole

data set and in communities of crop fields, fallows, steppificated meadows, and glades. This fact may be regarded as evidence that the size of the pool of adventive species does have an effect on the degree of saturation with these plants in local community areas. In communities on river shoals, N_a values vary significantly, but this has practically no effect on S_a (Table 2), which may be evidence for the presence of certain intrinsic factors controlling the spread of adventive species in such communities.

Attention should also be paid to the relatively weak and mainly positive correlation of S_a with the total coverage of herbaceous layer, both in the whole data set and in the majority of individual community types (Table 3). This fact contradicts the opinion that frequently disturbed, open communities are more vulnerable to invasion than closed communities.

As follows from Table 3, S_a strongly depends on the species-holding capacity of communities (S): the higher the S value, the greater the number of adventive species in local community areas. This may be evidence that environmental conditions favorable for native species are usually also favorable for adventive species and that abiotic factors, compared to biotic, are more effective in creating a barrier to community invasion by adventive species. The positive correlation of S_a with S is stronger in communities on river shoals; weaker in communities of meadows, glades, and fallows; and decreases almost to zero in communities of crop fields. This results agrees with the observation (Davies et al., 2007) that the positive correlation between the numbers of adventive and native species is usually stronger in communities formed in low-productive than in high-productive habitats.

Finally, S_a consistently shows a negative correlation with number of native species in large plots (N_n), although its strength varies depending on community type. The fact that S_a positively depends on S and negatively depends on N_n indicates that the number of adventive species in local community areas is contingent, among other factors, on the level of species completeness, which widely varies between the communities studied (Table 2, figure). The level of species completeness, being relatively high in many local areas of communities on river shoals, is generally medium or low in areas of crop field, fallow, and meadow communities. According to our data (Table 2), the species completeness of evolutionarily young segetal communities is not lower than in communities of steppificated meadows. Calculations show (figure) that, in the whole data set, S/N_n accounts for more than 30% of variance in S_a ($r = 0.571$, $R^2 = 0.326$, $n = 128$, $P < 0.001$), with S accounting for 25% of this variance ($r = 0.496$, $R^2 = 0.246$, $n = 128$, $P < 0.001$). Moreover, the effect of S and N_n on the number of adventive species is stronger in more complete communities of river shoals than in less complete communities of crop fields, fallow lands, and meadows (Table 3). This may be evidence that S/N_n is a limiting factor for adventive species only if its values remain below a certain critical level.

CONCLUSIONS

Thus, the results of our study show that variation in the degree of saturation with adventive species in local areas of herbaceous communities in the Western Caucasus is largely determined by the number of such species in larger areas, the species-holding capacity of communities, and the level of their species completeness. Among the communities studied, the highest resistance to adventive species invasion in small areas is characteristic of open cenoses on shoals along low-mountain river sections. Although their species pool is fairly rich in adventive plants, the number of such species in local areas is relatively small, which is largely due to a low species-holding capacity (abiotic barrier) and relatively high species completeness (biotic barrier) of plant communities on river shoals.

The degree of adventization in communities of steppificated meadows and glades is also relatively low. However, this is not the effect of biotic barrier (as it could be expected), because the level of species completeness in such communities is relatively low; in addition, the number of adventive species in their local areas positively correlates with their species-holding capacity. Our results show that a probable explanation to the low degree of saturation with adventive plants in meadow cenoses is that the number of such species capable of invading these communities is not sufficiently high in the study region.

As expected, the degree of saturation with adventive species (in local areas) in communities of fallow lands and crop fields has proved to be higher than in other herbaceous communities of the Western Caucasus. However, our analysis has neither shown that this is due to low total coverage of the herbaceous layer, nor confirmed the assumption concerning the very low level of species completeness in these cenoses (this level is at least equal to that in meadow communities). These results indicate that the high degree of saturation with adventive species in communities of crop fields and fallow lands is accounted for by the favorable combination of biotic and abiotic conditions for their growth (as follows from the lack of significant correlations between S_a, S, and Cov), relatively low species completeness of these cenoses, and great number of adventive plants in their species pools.

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