ISSN 1067-4136, Russian Journal of Ecology, 2010, Vol. 41, No. 3, pp. 229–236. © Pleiades Publishing, Ltd., 2010.
Original Russian Text © V.V. Akatov, T.V. Akatova, 2010, published in Ekologiya, 2010, No. 3, pp. 191–198.

Saturation and Invasion Resistance of Non-Interactive Plant Communities

V. V. Akatov[a] **and T. V. Akatova**[b]
[a] *Maikop State Technological University,*
ul. Pervomaiskaya 191, Maikop, 385000 Russia
e-mail: akatovmgti@mail.ru
[b] *Caucasian State Biosphere Reserve,*
ul. Sovetskaya 187, Maikop, 385000 Russia
e-mail: hookeria@mail.ru

Received March 27, 2008

Abstract—Open plant assemblages in shoals of western Caucasian rivers were used as examples to analyze the relationship between the species saturation and the number and total abundance of alien species in non-interactive communities. Invasion of exotic species into highly saturated communities has been demonstrated to be, on average, less probable than their invasion into unsaturated communities. A hypothesis explaining the relationship between these parameters has been put forward. According to the hypothesis, the number of alien species in a specific locality in a community is determined by their ratio to the number of native species in the species pools of these communities; and their mean abundance, by the ratio of the total number of species to the number of individuals in the localities. Both ratios are smaller in saturated biocenoses, which determines a relatively small admixture of alien species in them.

Key words: plant assemblages, river shoals, species pool, species richness, species saturation, invading species, invasibility, western Caucasus.

DOI: 10.1134/S1067413610030069

Communities where the number of species is smaller than the species carrying capacity of the environment are termed unsaturated (Rabotnov, 1983). It is currently believed that communities may be unsaturated with species because they are young (in terms of succession or evolution) or isolated, or they were damaged in the historical past (MacArthur and Wilson, 1963; Ricklefs and Schluter, 1993, Davis et al., 2005). More than 20 years ago, Rabotnov (1983) supposed that, since such communities are characterized by a lower intensity of interspecific interactions than saturated communities, they should be less resistant to invasion of exotic (alien) species. However, it was not until recent years that the problem of invasibility became connected with the discussion on the degree of species saturation/unsaturation of currently existing biotas (Ricklefs and Schluter, 1993; Sax and Brown, 2000; Moore et al., 2001; Brown and Peet, 2003; Davis et al., 2005; Gilbert and Lechowicz, 2005; Sax et al., 2005; Akatov et al., 2007). Comparisons of the degrees of adventity of insular and continental floras (Sax and Brown, 2000; Mirkin and Naumova, 2002; Sax et al., 2005) and evidence that most invasions occur without replacing native species (Ricklefs and Schluter, 1993; Sax and Gaines, 2003; Sax et al., 2005) served as arguments to support a high invasibility of unsaturated communities. In addition, theoretical analysis showed that unsaturation of many communities invaded by alien species is indirectly confirmed by a positive correlation between the numbers of invading and native species (Moore et al., 2001).

Although this line of research is obviously promising, it has not been paid sufficient attention thus far (Gilbert and Lechowicz, 2005). In particular, it remains unclear whether the degree of species saturation may affect the richness of alien species in non-interactive communities, i.e., the communities where local species extinction results more from abiotic disturbance than from competition for space and resources (Cornell and Lawton, 1992; Cornell, 1993).

The purpose of our study was to fill this gap. Open plant assemblages in shoals of western Caucasian mountain rivers containing different proportions of alien species were used as objects of analysis.

MATERIALS AND METHODS

Estimation of species saturation. If the species saturation of communities (plant groups) actually affects their resistance to invasion of alien species, this parameters should be expected to be significantly negatively correlated with the number (total abundance) of invading species growing in these communities.

There are several approaches to estimation of the species saturation of biological communities. The most accurate one is experimental or field observations on competitive exclusion (or absence of exclusion) of native species upon invasion of new species into a community (Rabotnov, 1983; He et al., 2005). In terms of this approach, the fact that most invasions do not entail replacement of native species (Ricklefs and Schluter, 1993; Sax and Gaines, 2003; Sax et al., 2005) suggests that many communities are unsaturated. The main drawback of this approach is that the degree of community saturation is estimated on the basis of invasions that have already occurred (whether successfully or not), so the estimate cannot be compared with the potential invasibility of the community.

We assume that the relative local species saturation of biocenoses in a plot with area A can be estimated by comparing the species richness values in this plot (N) and in a plot with a smaller area $a(S)$ (Akatov, 1995; Akatov et al., 2002, 2005a, 2005b).

Let N and S be functions with unknown structures:

$$\begin{aligned} N &= N(c, p), \\ S &= S(c, p), \end{aligned} \tag{1}$$

where c is a parameter determined by local processes (environmental conditions), and p is a parameter determined by regional processes (the species pool size).

There is much evidence that, with increasing species pool, the species richness of communities in smaller reaches the upper limit (species capacity) more rapidly than in larger areas (Terborgh and Faaborg, 1980; Shurin et al., 2000; He et al., 2005; Akatov et al., 2005b). Therefore, if the species pool is greater than a certain small value, changes in S will be determined by local processes alone, and the system of equations (1) should be written as

$$\begin{aligned} N &= N(c, p), \\ S &= S(c). \end{aligned} \tag{2}$$

Hence, if communities in larger areas are saturated ($N = N(c)$), then N and S will vary only in response to environmental changes, their N/S ratios being approximately equal. Conversely, considerable variation of N/S is most likely to result from the dependence of the number of species on local processes alone in smaller areas and on both local and regional processes in larger areas (system of equations (2)). Thus, the higher N/S, the higher the relative species saturation of communities in large areas (Akatov, 1995; Akatov et al., 2002; Akatov et al., 2005b).

Note that the index of species saturation of communities that we suggest here is inversely proportional to the mean occurrence of species of these communities in localities ($N/S = 1/F$, where F is the mean occurrence of the species). Therefore, communities (plant assemblages) with high species saturations should have lower mean occurrences (abundances) of the species forming them compared to unsaturated biocenoses. This agrees with the notion that, as the saturation increases, the community tends towards the maximum possible diversity at the minimum possible ecological space and number of individuals per species (Preston, 1962; MacArthur and Wilson, 1963; Markov and Naimark, 1994; Zherikhin et al., 2001; Kaspari et al., 2003).

The region and methods of collection of the empirical material. The material was collected on shoals of five mountain rivers in the western Caucasus (Shepsi, Psezuapse, Zapadnyi Dagomys, Belaya, and Malaya Laba) at elevations from 70 to 900 m a.s.l. Open plant assemblages of shoals of three mountain rivers on the southern macroslope of the western Caucasus (Shepsi, Psezuapse, and Zapadnyi Dagomys) were described at elevations from 70 to 200 m a.s.l. In the Belaya River valley (the northern macroslope), plant assemblages of shoals in two localities at elevations of 200 and 440 m a.s.l. were described; in the Malaya Laba River valley (the northern macroslope), the shoals studied were located at elevations of 800–900 m a.s.l. The total projective cover of the plant assemblages on all shoals studied was no larger than 25%. Their brief characteristics are given in Table 1.

Descriptions were performed in 15-m^2 areas, within which 20 regular 0.5-m^2 plots were set. In each plot, the total projective cover was estimated, and species were identified. The total number of examined and described areas of plant assemblages was 68, including 26 areas on the southern macroslope, 22 plots in the Belaya River valley, and 20 plots in the Malaya Laba River valley. Forty-one descriptions were performed in the lower mountain belt (50–200 m a.s.l.), and 27 descriptions, in the middle mountain belt (450–900 m a.s.l.).

The collected material was used to calculate the following parameters: the mean number of all species in 0.5-m^2 plots (S), total number of species (N), the numbers of native (S_n) and alien (S_i) species in 15-m^2 areas, the proportion of invading species among the total number of species in 15-m^2 areas (S_i/N), mean occurrences of invading (F_i) and native (F_n) species in small plots, and the current species saturation of the communities (N/S) (note that the saturation had increased compared to the initial level because of invasion of alien species). The total abundance of invading species in plant assemblages were estimated on the basis of the sum of their occurrences (in the given case, it could be calculated as the product of the number of invading species by their mean occurrence, S_iF_i).

RESULTS AND DISCUSSION

Results of field studies. The total number of invading species in the test plots on river shoals on the southern macroslope was 11. These were *Ambrosia artemisiifolia* L., *Erigeron canadensis* L. (*Conyza canadensis* (L.)

Table 1. Characteristics of plant assemblages of river shoals

Parameter	Rivers					
	Shepsi and Psezuapse	Shepsi	Shepsi and Zapadnyi Dagomys	Belaya		Malaya Laba
Elevation a.s.l., m	70–80	100–125	190–200	200	440	800–900
P	48	18	36	49	45	46
P_i	8	9	7	9	5	4
N	11–27	4–12	9–12	7–19	16–31	13–28
Number of descriptions	11	7	8	15	7	20
The most frequent invading species on shoals						
Ambrosia artemisiifolia L.	69(39)	57(15)	13(10)	93(25)	86(48)	5(5)
Erigeron canadensis L.	18(11)	14(20)	13(10)	80(38)	100(47)	95(71)
Erigeron annuus (L.) Pers.	4(5)	43(22)		40(7)	86(25)	60(13)
Bidens frondosa L.	22(18)	14(10)	6(10)	47(20)	14(5)	
Xanthium californicum Greene	11(10)	14(14)		60(7)		
Oenothera biennis L.				33(9)	43(57)	20(40)
Some native species of open communities that are common on shoals						
Polygonum persicaria L.	80(51)	85(38)	69(43)	53(59)		15(25)
Setaria glauca (L.) Beauv.	90(67)	86(52)	88(48)	7(15)		
Setaria viridis (L.) Beauv.	100(80)		88(58)	100(58)	57(69)	
Convolvulus arvensis L.	39(14)	29(10)	19(13)	47(13)		
Crepis setosa Hall. fil.	43(26)			53(58)		
Verbena officinalis L.	7(5)	14(10)	25(10)	40(8)		10(5)
Plantago major L.	21(12)	14(20)	13(10)	7(15)	43(10)	25(9)
Calamagrostis pseudophragmites (Hall. fil.) Koel.				20(5)	43(18)	70(68)
Trifolium repens L.				14(5)	14(15)	35(21)
Silene compacta Fischer ex Hornem					28(25)	30(36)
Some native species of close communities found on shoals						
Prunella vulgaris L.	18(12)	17(18)	6(10)	7(5)	9(18)	55(19)
Pyrethrum parthenifolium Wild.	39(16)		56(26)		86(32)	65(19)
Stachys officinalis (L.) Trev.	7(5)		6(10)			
Geranium robertianum L.	26(23)		19(10)			
Linaria pontica Kuprian.	6(5)	14(10)				
Hedera helix L.	8(5)	14(10)				
Galega officinalis L.	8(5)			7(5)		25(10)
Leontodon hispidus L.					57(8)	55(20)
Alchemilla oxysepala Juz.					14(5)	25(10)
Epilobium montanum L.						65(21)

Note: The constancy of species in 15-m^2 areas and the mean occurrence of species in 0.5-m^2 plots are indicated before parentheses and in parentheses, respectively. Designations: P, total number of plant species included into descriptions; P_i, total number of invading plant species included into descriptions; N, number of species in 15-m^2 areas.

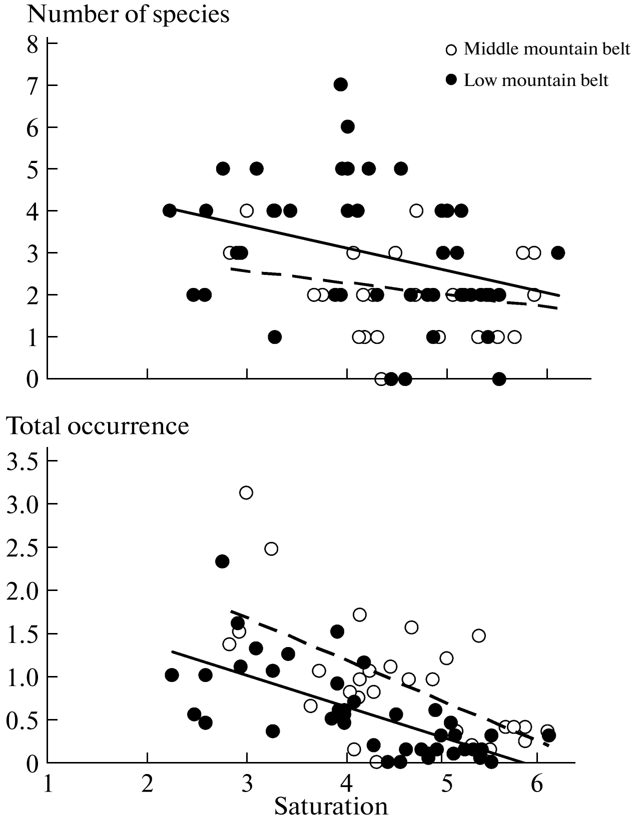

Fig. 1. Relationship between the species saturation (N/S) and the number (S_i) and total occurrence (S_iF_i) of invading species in plant assemblages of river shoals.

Cronq.), *E. annuus* (L.) Pers. (*Stenactis annua* (L.) Cass.), *Bidens frondosa* L., *Oxalis stricta* L., *Xanthium californicum* Greene, *Galinsoga parviflora* Cav., *Scrophularia peregrina* L., *Amaranthus retroflexus* L., *Oenothera biennis* L., and *Euphorbia nutans* Lagasca; the studied 15-m^2 areas contained from zero to seven invading species. *Ambrosia artemisiifolia, Erigeron canadensis*, and *Bidens frondosa* were the most frequent (Table 1).

Table 2. Relationship between the species saturation (N/S) and the number (S_i) and total occurrence (S_iF_i) of invading species in plant assemblages of river shoals

Plant assemblages	Parameter		n	r	P
	independent	dependent			
Total	N/S	S_i	68	−0.322	<0.01
	N/S	S_iF_i	68	−0.589	<0.001
Low mountain	N/S	S_i	41	−0.321	<0.05
	N/S	S_iF_i	41	−0.687	<0.001
Middle mountain	N/S	S_i	27	−0.247	
	N/S	S_iF_i	27	−0.663	<0.001

On the shoals of the lower Belaya River (200 m a.s.l.), we found nine invading species, *Ambrosia artemisiifolia* and *Erigeron canadensis* being the most frequent and abundant. *Bidens frondosa, Xanthium californicum, Erigeron annuus*, and *Oenothera biennis* were found slightly less frequently, and *Galinsoga parviflora, Amaranthus retroflexus*, and *Amorpha fruticosa* L. were rare. The number of invading species in the 15-m^2 areas varied from two to six.

On the shoals of the middle Belaya River (440 m a.s.l.), five invading species with approximately the same occurrence were found (*Ambrosia artemisiifolia, Erigeron canadensis, E. annuus, Bidens frondosa*, and *Oenothera biennis*). Two to four species were found in 15-m^2 test areas. We found four species on the shoals of the middle Malaya Laba River (*Ambrosia artemisiifolia, Erigeron canadensis, E. annuus*, and *Oenothera biennis*), *Erigeron canadensis* exhibiting the highest occurrence and abundance. The number of these species in 15-m^2 areas varied from zero to three.

Figure 1 and Table 2 show the results of analysis of the relationship between the current species saturation of plant assemblages (N/S), the number of invading species in 15-m^2 areas (S_i), and their total occurrence (S_iF_i). Taking into consideration the differences in the distribution of invading species, we separately analyzed the plant assemblages of shoals of the low- and middle- mountain belts (50–200 and 400–900 m a.s.l., respectively).

As can be seen in Fig. 1, the species saturation of the described plant assemblages (N/S) substantially varied, which may have been related to the characteristics of their formation in each particular locality (the species pool size, age and area of the shoal, distance of the assemblages from the source of diaspores, etc.). The variation range of this parameter was somewhat wider in the low mountain belt than in the middle mountain one. In addition, Fig. 1 and Table 2 demonstrate a significant negative correlation between the species saturation (N/S) and the total abundance (occurrence) of invading species (S_iF_i). In the pooled sample of plant assemblages, as well as in the assemblages located in the low mountain belt, the N/S value and the number of invading species (S_i) were significantly negatively correlated. Some assemblages with a relatively low species saturation contained as many as five to seven invading species (accounting for 30–60% of the total species richness) per 15-m^2 area, whereas assemblages with the highest N/S contained no more than three invading species accounting for less than 20% of the species richness of these assemblages (Fig. 2). The N/S and S_i of the plant assemblages of river shoals of the middle mountain belt were also negatively associated with each other, but the association was nonsignificant (Table 2). Thus, our results show that the assumption on a lower resistance of unsaturated communities to invasion of alien species is also true for non-interactive communities.

Figure 1 also shows that invading species growing on river shoals of the middle mountain belt reached, on average, a higher total abundance at the same species saturation than those growing in the low mountain belt. In addition, the mean occurrence of invading species was lower than that of native ones in the middle mountain belt and higher than it in the middle mountain belt (Fig. 2). In seeking to explain this difference, we compared the ecological structures of the pools of native plant assemblages located at different elevations. With increasing elevation (a.s.l.), the proportion of species characteristic of open habitats (disturbed and arable lands and shoals themselves) decreased, and, the proportion of the species that had come from dense communities (forests, meadows, etc.) correspondingly increased. Fore example, plant communities located below 60 m a.s.l. on the southern macroslope included more than 60% of species characteristic of open habitats; at elevations of 60–125 m, their proportion was 43–53%; at elevations about 200 m, 36% (Akatov and Akatova, 2006). On the northern macroslope, the proportion of species that had migrated to shoals from open habitats was 63, 46, and only 20% at elevations of about 200, about 400, and 800–900 m, respectively. This is most likely to have been related to differences in the degree of disturbance of plant communities on river banks.

These results suggest that native species of open habitats are more competitive with respect to alien species than native species of forest and meadow communities are, which largely determines the relatively high abundance of the few alien species in plant assemblages of river shoals of the middle mountain belt. Therefore, not only the species saturation of open communities, but also biological and autecological characteristics (the capacity for dispersal and the degree of adaptation to the given habitats) determine the susceptibility of these communities (assemblages) to the penetration and expansion of alien species.

The hypothesis on ratio between species pools. A question arises as to what mechanisms underlie the relationship between the species saturation of communities and the proportion of invading species in them. Most current hypotheses and models relate this phenomenon to the presence of unused resources and a lower intensity of competition between species for these resources in unsaturated biocenoses (Elton, 1958; Rabotnov, 1983; Moore et al., 2001; Berdnikov et al., 2002). However, the alternative explanation presented below may better explain this relationship in non-interactive communities. The explanation can be reduced to the following assumptions:

(1) All other conditions (the species capacity, community area, degree of isolation, etc,) being the same, the community saturation is determined by the size of their species pool: the larger the species pool, the higher the saturation (MacArthur and Wilson, 1963; Terborgh and Faaborg, 1980; Ricklefs, 1987; He et al., 2005; Cornell, 1993; etc.). Hence, the reverse should also be true: all other conditions being the same, saturated biocenoses have larger species pools than unsaturated ones.

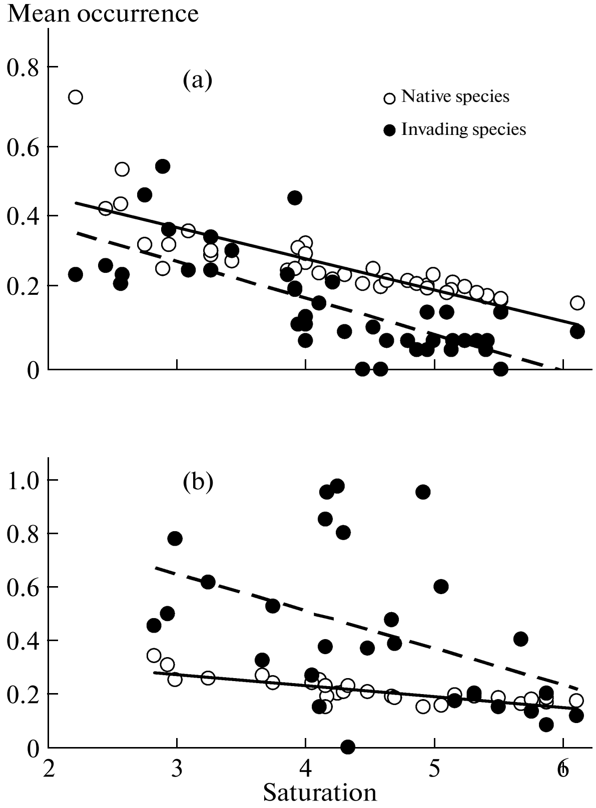

Fig. 2. Relationship between the species saturation (N/S) of plant assemblages of river shoals and the mean numbers of native (F_n) and invading (F_i) species in them. Plant assemblages: (a) low mountain belt; (b) middle mountain belt.

(2) All other conditions (the total population density, degree of dominance, etc,) being the same, communities (plant assemblages) with a higher species saturation are characterized by lower occurrences (population sizes) of the constituent species than unsaturated communities are.

(3) Invading species may be, on average, either more or less abundant than native species; however, as evident from Fig. 2 and Table 3, they respond to an increase in the community saturation in the same way: their mean population sizes (occurrences) decrease. This increases the risk of their local extinction, especially in an unpredictably varying environment (MacArthur and Wilson, 1963; Shaffer, 1981; Hanski, 1982; Hanski et al., 1996; etc.).

(4) The number of alien species capable of growing in communities of different types being the same, their proportion in the species pools of saturated biocenoses is smaller than in those of less saturated ones, which makes colonization (or recolonization) of areas of saturated communities by these species less probable

Table 3. Relationship between the species saturation (N/S) of plant assemblages of river shoals and the mean numbers of native (F_n) and invading (F_i) species in them

Plant assemblages	Parameter		n	r	P
	independent	dependent			
Low mountain	N/S	F_n	41	−0.808	<0.001
	N/S	F_i	41	−0.734	<0.001
Middle mountain	N/S	F_n	27	−0.811	<0.001
	N/S	F_i	27	−0.439	<0.05

compared to areas occupied by unsaturated communities.

(5) The decrease in the mean population size and the number of alien species along the gradient of saturation determine a decrease in the total number of individuals and the occurrence.

Let us illustrate these statements by a variant of MacArthur and Wilson's (1963) insular ecology model modified by He et al. (2005) for analyzing the relationship between the species pool and the local richness of non-interactive communities. This model is based on the assumptions that (a) all species constituting the species pool have the same capacity for dispersal and survival in colonized areas and (b) both immigration and extinction of species are stochastic.

According to MacArthur and Wilson's theory, the number of species on an island or in another locality (S) is determined by the equilibrium between their extinction and immigration. It includes two main equations. The first one describes the dependence of the immigration rate (I) on the size of the species pool (P) and the number of species that are already present on an island or in a locality (S):

$$I = I_0 a^v (1 - S/P), \tag{3}$$

where I_0 is the maximum immigration rate and v is the parameter describing the effect of the area of the island or locality (a) on I_0.

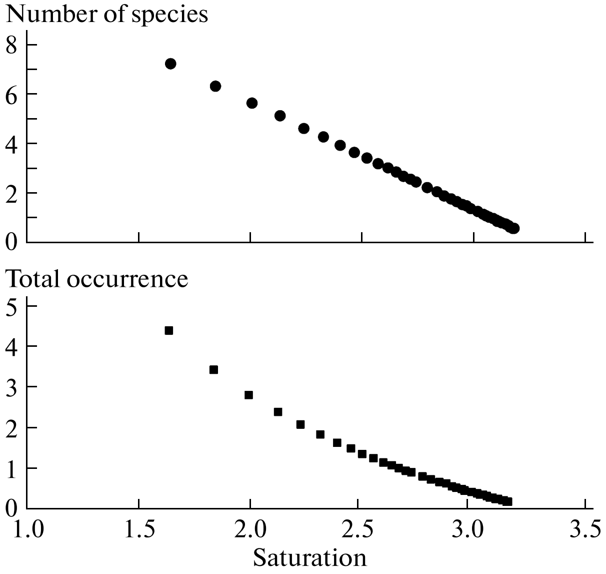

Fig. 3. Relationship between the species saturation (N/S) and the number (S_i) and total occurrence (S_iF_i) of invading species in model communities.

The second equation describes the dependence of the extinction rate on the size of the island (locality) and the number of species that are already present on the island (locality):

$$E = E_0 a^{-x} S, \tag{4}$$

where E_0 and x are constants.

On the basis of these equations, the ratio between the local species richness of communities (S) and the sizes of their species pools (P) in the state of equilibrium between extinction and immigration ($I = E$) can be written as follows:

$$S = a^z P/(a^z + \delta P), \tag{5}$$

where $z = v + x$ and $\delta = E_0/I_0$ (the higher this parameter, the more "severe" the environmental conditions and the greater the role of this factor in determining S).

If invading and native species are ecologically equivalent, the proportion of invading species in communities (S_i/S) is proportional to their proportion in the species pools of these communities (P_i/P) (Fridley et al., 2004). Then, the number of these species in localities of communities with area a may be calculated as

$$S_i = SP_i/P = a^z P_i/(a^z + \delta P). \tag{6}$$

Figure 3 shows the relationship between the species saturation of model communities (N/S) and the number (S_i) and total occurrence (S_iF_i) of invading species in them that is expected according to Eqs. (5) and (6). When plotting the model curves, we assumed that the size of the species pool of alien species (P_i) in communities with different combinations of the P, N/S, and δ values is constant (10 species). To determine the model N/S values, we compared the number of species in 15- and 0.5-m^2 plots. The values of other model parameters were the following: P varied from 20 to 150, δ varied from 0.05 to 0.3, and z was 0.35 (this value of z was used by the authors of the model (He et al., 2005)). The number of variants of such combinations was 56. It is also assumed that the total occurrence of invading species in communities corresponds to the number of these species in plots with $a = 0.5$ m^2 (S) (this follows from the equation $S = FN$, where F and FN are the mean and total occurrences of species in plots with $a = 0.5$ m^2, respectively).

As evident from Fig. 3, the values of both parameters characterizing the proportion of invading species in communities clearly tend to decrease with increasing N/S. This agrees with the results of field studies described above and indicates that the number and abundance of these species in more saturated communities are smaller than in less saturated ones if the numbers of invading species in the species pools of the communities or, in other words, the intensities of action of this factor on the communities are equal.

Thus, it is not necessary to analyze the intensity of interspecific interactions to explain why saturated biocenoses are highly resistant to invasion of alien species. The assumptions that alien and native species are ecologically equivalent and their immigration and extinction in plots occupied by the communities are stochastic. Our results indicate that the number of alien species in a specific plot is determined by its ratio to the number of native species; and their mean abundance, by the ratio of the total number of species to the number of individuals in the plots. Since both ratios are always relatively lower in more saturated biocenoses, a lower total abundance of alien species should be expected there.

However, our studies have also demonstrated that the assumption that native and alien species are, on average, ecologically equivalent, is an oversimplification. Therefore, not only the level of species saturation of open communities, but also the biological and autecological characteristics of the constituent native species affect the susceptibility of these communities to the penetration and expansion of alien species.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic Research, project no. 07-04-00 449.

REFERENCES

Akatov, V.V., Analysis of Floristic Incompleteness of Phytocenoses As a Method of Testing for the Insular Effect, *Bot. Zh.*, 1995, vol. 80, no. 4, pp. 49–64.

Akatov, V.V. and Akatova, T.V., Composition and Species Richness of Plant Groups on River Shoals in the Sochi National Park, in *Nauchnye trudy Sochinskogo natsional'nogo parka* (Scientific Works of the Sochi National Park), Moscow, 2006, issue 2, pp. 140–147.

Akatov, V.V., Chefranov, S.G., and Akatova, T.V., The Species Pool Hypothesis: The necessity to Shift Emphasis, *Zh. Obshch. Biol.*, 2002, vol. 63, no. 2, pp. 112–121.

Akatov, V.V., Chefranov, S.G., and Akatova, T.V., The Role of Historical Processes in Determining Tree Species Richness in Forests of the Western Caucasus, *Zh. Obshch. Biol.*, 2005a, vol. 66, no. 6, pp. 479–490.

Akatov, V., Chefranov, S., and Akatova, T., The Relationship between Local Species Richness and Species Pool: A Case Study from the High Mountains of the Greater Caucasus, *Plant Ecol.*, 2005b, vol. 181, no. 1, pp. 9–22.

Akatov, V.V., Akatova, T.V., Zagurnaya, Yu.S., et al., Species Saturation Level and Invasibility of Plant Communities in the Western Caucasus: Introduction to the Problem, in *Ustoichivost' ekonomicheskikh i ekologicheskikh sistem. Regional'nyi aspekt* (Stability of Economic and Ecological Systems: Regional Aspects), Maikop, 2007, pp. 84–100.

Berdnikov, S.V., Kuznetsova, I.S., and Selyutin, V.V., Mathematic Modeling of Alien Population Invasion into Established Plant Communities, *Izv. Vuzov. Severo-Kavkazskii Region. Estestvennye Nauki*, 2002, no. 2 (118), pp. 72–80.

Brown, R.L. and Peet, R.K., Diversity and Invasibility of Southern Appalachian Plant Communities, *Ecology*, 2003, vol. 84, no. 1, pp. 32–39.

Cornell, H.V., Unsaturated Patterns in Species Assemblage: The Role of Regional Processes in Setting Local Species Richness, in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D., Eds., Chicago: Univ. of Chicago Press, 1993, pp. 243–253.

Cornell, H.V. and Lawton, J.H., Species Interactions, Local and Regional Processes, and Limits to the Richness of Ecological Communities: A Theoretical Perspective, *J. Anim. Ecol.*, 1992, vol. 61, pp. 1–12.

Davis, M.A., Thompson, K., and Grime, J.P., Invasibility: The Local Mechanism Driving Community Assembly and Species Diversity, *Ecography,* 2005, vol. 28, no. 5, pp. 696–704.

Elton, C.S., *The Ecology of Invasions by Animals and Plants*, London: Methuen, 1958.

Fridley, J.D., Brown, R.L.,, and Bruno, J.E., Null Models of Exotic Invasion and Scale-Dependent Patterns of Native and Exotic Species Richness, *Ecology,* 2004, vol. 85, no. 12, pp. 3215–3222.

Gilbert, B. and Lechowicz, M.J., Invasibility and Abiotic Gradients: The Positive Correlation between Native and Exotic Plant Diversity, *Ecology,* 2005, vol. 86, no. 7, pp. 1848–1855.

Hanski, I., Dynamics of Regional Distribution: The Core and Satellite Species Hypothesis, *Oikos,* 1982, vol. 38, pp. 210–221.

Hanski, I., Moilanen, A., and Gyllenberg, M., Minimum Viable Metapopulation Size, *Am. Nat.*, 1996, vol. 147, no. 4, pp. 527–541.

He, F., Gaston, K.J., Connor, E.F., and Srivastava, D.S., The Local–Regional Relationship: Immigration, Extinction, and Scale, *Ecology*, 2005, vol. 86, pp. 360–365.

Kaspari, M., Yuan, M., and Lecanne, A., Spatial Grain and the Causes of Regional Diversity Gradients in Ants, *Am. Nat.*, 2003, vol. 161, no. 3, pp. 459–477.

MacArthur, R.H. and Wilson, E.O., An Equilibrium Theory of Insular Zoogeography, *Evolution*, 1963, vol. 17, no. 4, pp. 373–387.

Markov, A.V. and Naimark, E.B., Selective Extinction of Specialized Taxa and Its Role in Evolution of the Biota, *Zh. Obshch. Biol.*, 1994, vol. 55, no. 6, pp. 673–683.

Mirkin, B.M. and Naumova, L.G., Adventization of Vegetation A View through the Prism of Modern Ecology, *Zh. Obshch. Biol.*, 2002, vol. 63, no. 6, pp. 500–508.

Moore J.L., Mouquet, N., Lawton, J.H, and Loreau, M., Coexistence, Saturation and Invasion Resistance in Simulated Plant Sssemblages, *Oikos,* 2001, vol. 94, pp. 303–314.

Preston, F.W., The Canonical Distribution of Commonness and Rarity, *Ecology*, 1962, vol. 13, pp. 185–215, 410–432.

Rabotnov, T.A., *Fitotsenologiya* (Phytocenology), Moscow: Mosk. Gos. Univ., 1983.

Ricklefs, R.E., Community Diversity: Relative Roles of Local and Regional Processes, *Science*, 1987, vol. 235, pp. 167–171.

Ricklefs, R.E. and Schluter, D., Species Diversity: Regional and Historical Influences, in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, Ricklefs, R.E. and Schluter, D., Eds., Chicago: Univ. of Chicago Press, 1993, pp. 350–362.

Sax, D.F. and Brown, J.H., The Paradox of Invasion, *Global Ecol. Biogeogr.*, 2000, vol. 9, pp. 363–371.

Sax, D.F. and Gaines, S.D., Species Diversity: From Global Decreases to Local Increases, *Trends Ecol. Evol.,* 2003, vol. 18, no. 11, pp. 561–566.

Sax, D.F., Brown, J.H., White, E., and Gaines, S.D., The Dynamics of Species Invasions: Insights into the Mechanisms That Limit Species Diversity, in *Species Invasions: Insights Into Ecology, Evolution, and Biogeography*, Sax, D.F. and Gaines, S.D., Eds., Sunderland, MA: Sinauer Assoc., 2005, pp. 447–465.

Shaffer, M.L., Minimum Population Sizes for Species Conservation, *Bioscience*, 1981, vol. 31, pp. 131–134.

Shurin, J.B., Havel, J.E., Leibold, M.A., and Pinel-Alloul, B., Local and Regional Zooplankton Species Richness: A Scale-Independent Test for Saturation, *Ecology*, 2000, vol. 81, no. 11, pp. 3062–3073.

Terborgh, J.W. and Faaborg, J., Saturation of Bird Communities in the West Indies, *Am. Nat.*, 1980, vol. 116, pp. 178–195.

Zherikhin, V.V., Krasilov, V.A., Leonova, T.B., et al., Models of Biosphere Evolution Based on Phylocenogenesis (Evolution of Communities), in *Global'nye izmeneniya prirodnoi sredy* (Global Changes in the Natural Environment), Novosibirsk, 2001, pp. 265–273.