Species Richness of Tree and Shrub Layers in Riparian Forests of the Western Caucasus Dominated by Alien Species

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Received Match 29, 2011

Abstract—The consequences of replacement of native dominants by alien species (*Ailanthus altissima, Ficus carica, Robinia pseudoacacia, Acer negundo*, and *Amorpha fruticosa*) in the tree and shrub layers have been studied in riparian forests of the Western Caucasus. The results show that the invasive dominant species do not always achieve higher abundance, compared with native dominants. When this is the case, however, the dominance of alien species as stronger competitors leads to reduction in the species richness of communities, because they not only intercept the greater part of resources from the environment but also provoke increasingly strict partitioning of remaining resources among associated species.

Keywords: alien species, tree layer, shrub layer, riparian forests, dominants, species richness, the Western Caucasus

DOI: 10.1134/S1067413612040030

An important aspect of the problem of plant cover adventization concerns situations when alien species gain dominance in phytocenoses. This usually takes place after serious disturbances of native communities (Reinhart, Greene, and Callaway, 2005; Smith et al., 2009), and it cannot be excluded that alien dominants may manifest certain properties having an adverse effect on the species richness of phytocenoses.

For example, alien species may prove to be stronger competitors than native species commonly dominating in given habitats and, consequently, exceed them in abundance and dominance level (Meiners, Pickett, and Cadenasso, 2001; Silliman and Bertness, 2004; Hejda, Pysek, and Jarok, 2009). The higher this level, the smaller the amount of resources available to associated species and, therefore, the lower the possible abundance and species richness of communities (Mirkin and Naumova, 1998; McKane et al., 2002; Kunte, 2008). The significance of this factor for species richness is confirmed by the facts of increase in the diversity of different types of communities after the removal or suppression of dominants or reduction of their diversity after an increase in the abundance of dominants (Bobbink and Willems, 1987; Kunte, 2008; Vasilevich, 2009). Therefore, the replacement of native dominants by more competitive alien dominants in plant communities may have serious consequences for the species richness of both native plants (Meiners, Pickett, and Cadenasso, 2001; Silliman and Bertness, 2004; Hejda, Pysek, and Jarok, 2009) and alien plants (Alvarez and Cushman, 2002; Hulme and Bremner, 2006).

Moreover, the environment-forming activities of some alien species (selective utilization of mineral nutrients, alteration of light regime and physicochemical soil properties, allelopathy, etc.) may interfere with the growth of native species commonly occurring in a given habitat type (Callaway and Ridenour, 2004; Reinhart, Greene, and Callaway, 2005; Hulme and Bremner, 2006). As a result, communities with prevalence of alien plants may consist of a smaller number of species, compared to the initial communities, even when the relative abundance of alien and native species is equal.

It should be noted, however, that the concept of significant dependence of phytocenosis species richness on specific bioecological features of dominant species accounting for their superiority over other plants is apparently not applicable to all communities and situations. In particular, this follows from the results of long-term observations on communities of different systematic groups in which the species abundance distribution and species richness of certain cenoses are relatively stable, whereas their species composition and ranks of particular species considerably change with time (Brown et al., 2001; Nally, 2007). Such observations provided a basis for the hypothesis that the level of dominance, species abundance distribution, and species richness may be regarded as emergent community properties (Brown et al., 2001; Raybaud et al., 2009; etc.). In this context, the proportion of total available resources utilized by the most abundant (dominant) species is not a particular quantity depending on bioecological features of

plants or on some random factors, but it rather reflects the general pattern of distribution of niche space among species under given conditions. If this hypothesis is true, the replacement of native dominants by alien species should neither lead to a significant increase in the level of dominance neither have any serious consequences for the species diversity of communities.

There is also the opinion that the level of dominance does not determine species richness but rather depends on it or, more precisely, on the community species pool (Vasilevich, 1991; Chernov, 2005), and the size of this pool, in turn, can be determined factors acting on a local or regional scale (Ricklefs, 1987). The larger the pool and the higher the species richness of cenoses, the greater the number of species capable of reaching high abundance and the lower the level of their individual dominance in particular areas (Vasilevich, 1991). Therefore, the enrichment of the community species pool with alien plants (particularly those capable of reaching high abundance) should lead to a decrease, rather than increase, in the level of dominance in this community.

The bioecological features of alien species and the complex, not yet completely understood nature of dominance (Akatov and Perevozov, 2011) make it difficult to predict probable consequences of the replacement of native by alien dominants. This follows from the results of field studies, which show that alien dominants can have a significant effect on the species richness and composition of phytocenoses (Meiners, Pickett, and Cadenasso, 2001; Silliman and Bertness, 2004; Reinhart, Greene, and Callaway, 2005; Hejda, Pysek, and Jarok, 2009) and, on the other hand, that such an effect may be absent (Houlahan and Findlay, 2004; Sagoff, 2005; Hulme and Bremner, 2006), even when dealing with invasions of the same species but in different areas (Hejda and Pysek, 2006; Mills et al., 2009). On the whole, published data on this problem are scarce, despite its theoretical and practical importance.

The purpose of this study was to analyze the consequences of replacement of native by alien dominants for the species richness of tree and shrub layers in riparian forests of the Western Caucasus.

MATERIAL AND METHODS

In the course of field studies in the Western Caucasus (2007−2010), we revealed and described 64 plots (300 m² each) where the tree layer of riparian forests was dominated by alien species (*Robinia pseudoacacia*, 40 plots along the Belaya River; *Acer negundo*, 14 plots along the Pshish River; *Ailanthus altissima* and *Ficus carica*, 7 and 3 plots, respectively, along rivers of the Black Sea Region), and also 90 15-m² plots with dominance of *Amorpha fruticosa* in the shrub layer (along the Belaya River). Below, these communities are referred to as invaded.

The above dominants found in riparian forests are escaped introduced species native to North America (*Robinia pseudoacacia, Acer negundo*, and *Amorpha fruticosa*) or East Asia (*Ailanthus altissima*), where they grow in temperate or moderately warm bioclimatic zones, but the range of *Acer negundo* also extends to the boreal zone (Pilipenko, 1978). The question concerning the region of *Ficus carica* origin is debatable. This species, which was introduced in cultivation in the Antique period, has spread far beyond the boundaries of its initial range due to human activities. Having escaped to the wild, it is now a component of various natural forest cenoses in subtropical and moderately warm regions of Asia and Europe, including Transcaucasia.

Data on invaded communities were compared with those on similar communities dominated by native species growing either in the same forest areas or in analogous habitats located elsewhere (taken as a reference communities). In particular, specific features of the tree layer in riparian forests dominated by *Robinia pseudoacacia* were evaluated in comparison with two groups of forest plots (42 plots each) dominated by native species (*Populus nigra, Alnus incana*, and *Salix alba*) and located in identical habitats of the same Belaya River valley at similar elevations (150−200 m a.s.l.). For forests dominated by *Acer negundo*, we used 14 reference plots in riparian forests dominated by *Salix alba* and *Alnus incana* in the Pshish River basin (100−240 m a.s.l.). For forests dominated by *Ailanthus altissima* (the Sochi, Matsesta, and Tekos river valleys, 17−130 m a.s.l.), three groups of reference plots (seven plots each) were selected in Sochi, Matsesta, Shakhe, and Ashe river valleys (100−130 m a.s.l.), with *Alnus glutinosa* dominating in two groups and *Alnus incana* in one group. Three plots dominated by *Ficus carica* in riparian forest on the steep right bank of the Mzymta River (133 m a.s.l.) were compared with two groups of three and four plots located on the same bank between 110 and 185 m a.s.l. and one group of three plots in similar habitats of the Shakhe River valley (102 m a.s.l.). *Alnus glutinosa* was dominant in all these plots except one, where *Alnus glutinosa* dominated.

To evaluate specific features of the shrub layer dominated by *Amorpha fruticosa*, we used 85 reference plots with dominance of native shrub species (*Swida australis, Corylus avellana, Euonymus europaea*, and *Ligustrum vulgare*) located in the same riparian forest areas along the Belaya River (150−200 m a.s.l.).

Relev@es of the tree stand in 300-m² plots included brief characteristics of forest phytocenosis and counts of all individuals of tree species with a breast-height diameter of more than 6 cm. Relev@es of the shrub layer were made in 15-m² plots arranged in groups of 20, where all shrubs taller than 0.5 m and young trees 0.5−2 m high were counted. The abundance of species was estimated from the number of individuals. Parameters used to compare communities dominated by alien and native species were as follows: *N*, the average

Table 1. Relationships between the level of dominance and species richness in the tree and shrub layer of riparian forest phytocenoses of the Western Caucasus

Communities dominated by alien species and corresponding reference communities	n	r	R^2	P
Ailanthus altissima	28	−0.731	0.535	<0.001
Ficus carica	13	−0.718	0.516	<0.01
Robinia pseudoacacia	124	−0.677	0.482	<0.001
Acer negundo	28	−0.662	0.438	<0.001
Amorpha fruticosa	175	−0.777	0.603	<0.001

Table 2. Characteristics of tree and shrub layers in riparian forests of the Western Caucasus dominated by alien or native species

Dominant species	n	N	$K_1 (K_{1\,max})$	S_l	S_r	D_c
Ailanthus altissima	7	26.86	0.74 (0.95)	2.71	7	4.05
Native species	7	24.29	0.88 (0.96)	2.57	6	2.07
Native species	7	26.29	0.85 (1.00)	2.29	5	1.74
Native species	7	24.00	0.95 (1.00)	2.00	5	0.93
Ficus carica	3	44.67	0.52 (0.66)	7.67	14	3.29
Native species	3	36.33	0.50 (0.63)	6.67	13	3.49
Native species	4	38.75	0.51 (0.63)	6.00	11	4.22
Native species	3	25.00	0.64 (0.83)	5.33	10	2.02
Robinia pseudoacacia	40	27.53	0.63 (1.00)	3.85	25	2.95
Native species	42	26.02	0.61 (1.00)	4.05	17	3.40
Native species	42	24.74	0.60 (0.98)	4.00	22	3.33
Acer negundo	14	27.79	0.63 (0.95)	3.35	12	4.90
Native species	14	24.71	0.51 (0.72)	4.07	14	5.33
Amorpha fruticosa	90	25.93	0.87 (1.00)	2.47	22	1.74
Native species	85	24.76	0.61 (0.95)	4.65	30	2.65

Note: (n) the number of plots, (N) the average number of trees (shrubs) per plot, ($K1$) the ratio of the number of trees (shrubs) of dominant species to the total number of trees (shrubs), (K_{1max}) the maximum value of this index, (S_l) the average number of species per plot, (S_r) the total number of species in groups of plots, and (D_c) the average density of trees (shrubs) of associated species per plot.

number of trees or shrubs per plot; K_1, the proportion of dominant individuals among the total number of individuals (the Berger–Parker dominance index) (Lebedeva and Krivolutskii, 2002); S_l, the average number of species in the plots; S_r, the total number of species in a group of plots; and D_c the average density of associated species in the plots. The patterns of species abundance distribution in plots (communities) dominated by alien and native species were compared by plotting and analyzing average logarithmic rank–abundance diagrams for the groups of plots, with the X axis showing the abundance rank (the most abundant species is given rank 1, the second most abundant is 2, etc.) and the Y axis showing the average abundance of corresponding species on a log scale (Lebedeva and Krivolutskii, 2002).

RESULTS AND DISCUSSION

Data on characteristics of forest plots dominated by alien and native tree and shrub species are summarized in Tables 1–6 and Figs. 1, 2. In particular, Table 1 shows data on the degree of correlation between the level of dominance and the species richness of plant communities, with the groups of plots dominated by alien and native species being considered together. It can be seen that, in all cases, these parameters showed a significant negative correlation with each other. Therefore, it could be expected that strong dominance of alien species in communities would results in reduction of their species diversity. Let us consider this issue using the examples of forest plots described in the study area.

Table 3. Parameters of the logarithmic rank–abundance model for dominant species ($\log y = \log a + x \log b$)

Dominant species	n	a	b	R^2
Ailanthus altissima	7	131.72	−1.72	0.98
Native species	7	87.76	−1.67	0.98
Native species	7	95.16	−1.60	0.97
Native species	7	148.29	−2.19	0.94
Ficus carica	3	27.60	−0.50	0.97
Native species	3	16.99	−0.45	0.93
Native species	4	31.57	−0.60	0.99
Native species	3	18.03	−0.61	0.99
Robinia pseudoacacia	40	24.63	−0.76	0.98
Native species	42	31.34	−0.82	0.99
Native species	42	31.21	−0.82	0.99
Acer negundo	14	43.35	−0.99	0.98
Native species	14	18.76	−0.61	0.98
Amorpha fruticosa	90	64.17	−1.43	0.99
Native species	85	22.86	−0.67	0.99

Table 4. Species composition of the tree layer in riparian forests of the Western Caucasus dominated by alien species (*Ficus carica* and *Ailanthus altissima*) or native species (average number of trees per 300-m^2 plot)

Species composition	Communities							
	with *Ficus carica*				with *Ailanthus altissima*			
	Ref	Ref	Ref	Aln	Ref	Ref	Ref	Aln
Number of plots	3	4	3	3	7	7	7	7
Adventive dominants								
Ficus carica L.	0.33	0.25	2.00	23.00	0.14	1.00		
Ailanthus altissima (Miller) Swingle		0.25			1.57			19.86
Native dominants								
Alnus glutinosa (L.) Gaertner	16.67	19.75	16.00	2.33	21.29	20.29		3.57
Alnus incana (L.) Moench	7.33	0.25					22.71	
Most common associated species								
Paulovnia tomentosa (Thunb.) Steudel	2.33	5.25		3.33	0.43			0.29
Salix alba L.	1.67	5.50		1.67			0.57	
Ulmus glabra Hudson	1.33	0.75	0.33	4.67				
Corylus avellana L.		0.25	1.00	0.67		0.57	0.29	
Acer campestre L.			0.33	0.33			0.29	0.14

Note: (Aln) communities dominated by alien species; (Ref) communities dominated by native species (here and in Tables 5, 6).

Characteristics of the tree layer in riparian forest plots dominated by *Ailanthus altissima* on the southern macroslope of the Western Caucasus and in three groups of corresponding reference plots are given in Tables 2–4 and Fig. 1. As follows from Table 2, the test plots hardly differed from the reference plots in tree stand density but had a lower level of dominance and higher species richness (S_l and S_r) and average density of associated species. The rank distribution of species abundance in invaded and reference communities had similar patterns (Fig. 1). Moreover, the rank–abundance ratio in three groups of plots were adequately described by a linear function ($R_2 = 0.97–0.98$; Table 3), indicating that the structure of species abundance conformed to the geometric model. According to the niche pre-emption hypothesis (Whittaker,

Table 5. Species composition of the tree layer in riparian forests of the Western Caucasus dominated by alien species (*Robinia pseudoacacia* and *Acer negundo*) or native species (average number of trees per 300-m^2 plot)

Species composition	Communities				
	with *Robinia pseudoacacia*			with *Acer negundo*	
	Ref	Ref	Aln	Ref	Aln
Number of plots	42	42	40	14	14
Adventive dominants					
Robinia pseudoacacia L.	2.17	2.02	18.78		
Acer negundo L.	0.14	0.14	0.03	4.86	17.50
Native dominants					
Populus nigra L.	9.10	8.79	1.75	0.21	
Alnus incana (L.) Moench	4.31	5.00	1.58	2.79	0.71
Salix alba L.	3.95	5.02	2.08	10.64	4.71
Most common associated species					
Populus alba L.	1.12	1.33	0.70	1.29	1.36
Fraxinus excelsior L.	1.02	1.21	0.25	0.71	1.00
Salix triandra L.	0.88	1.24	0.05	0.43	0.14
Acer campestre L.	0.26	0.14	0.23	0.50	0.14

1980), this can be regarded as evidence that each in the series of species arranged in order of decreasing abundance (increasing rank) utilizes a constant (*K*th) part of remaining community resources.

Plots of riparian forests dominated by *Ficus carica* in the Mzymta River valley were similar to reference plots in the level of dominance and average density of associated species but had higher values of tree stand

Table 6. Species composition of the shrub layer in riparian forests of the Western Caucasus dominated by *Amorpha fruticosa* or native species (average number of shrubs per 15-m^2 plot)

Species composition	Communities	
	Ref	Aln
Number of plots	85	90
Adventive dominant		
Amorpha fruticosa L.	1.44	22.98
Native dominants		
Cornus australis C.A.Meyer	7.61	1.43
Euonymus europaea L.	6.92	
Most common associated species		
Acer campestre L.	1.42	0.14
Corylus avellana L.	1.33	0.02
Ligustrum vulgare L.	1.04	0.01
Alnus incana (L.) Moench	0.92	0.10
Prunus cerastifera Ehrh.	0.45	0.20
Viburnum opulus L.	0.20	0.04

density and species richness (Table 2). The rank distribution of species in invaded and reference communities had similar patterns (Fig. 1).

Characteristics of the tree layer in riparian forest plots with dominance of *Robinia pseudoacacia* in the Belaya River valley (the northern macroslope of the Western Caucasus) and in two groups of reference plots are given in Tables 2, 3, 5 and Fig. 2. It can be seen that these barely differed in the majority of parameters, but plots in invaded communities on the whole included a somewhat greater number of species, compared to plots dominated by native species, and the average density of species in invaded communities was consequently lower (Tables 2, 5). The patterns of rank distribution of species in the invaded and reference communities was similar and well conformed to the geometric model (Fig. 2, Table 3).

In plots of riparian forests dominated by *Acer negundo* (the Pshish River valley), tree stand density and dominance level (both average and maximum) were higher, while species richness and the average density of associated species were lower than in reference plots (Tables 2, 5). The rank−abundance ratio in both groups of plots is adequately described by a linear function ($R_2 = 0.98$; Table 3), but the diagram for invaded communities is steeper. This is evidence that tree species in communities dominated by *Acer negundo* were on average characterized by lower abundance than species of corresponding ranks in communities with native dominants.

In plots where *Amorpha fruticosa* prevailed in the shrub layer, the level of dominance was higher, while species richness and average density of associated spe-
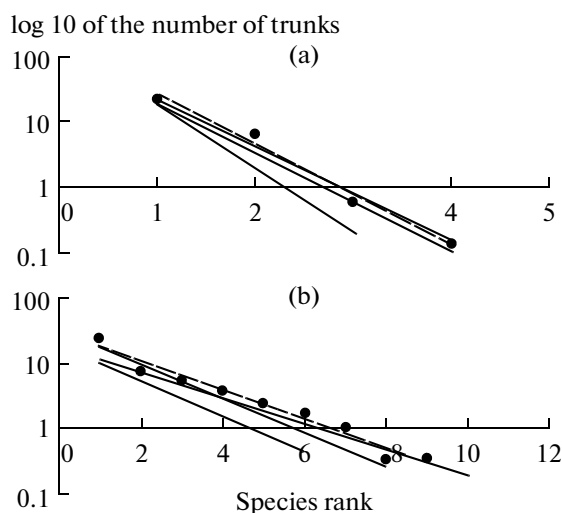
log 10 of the number of trunks

Fig. 1. Logarithmic rank–abundance diagrams for species recorded in the tree layer of riparian forests in plots dominated by (a) *Ailanthus altissima* or (b) *Ficus carica* and in reference plots dominated by native tree species. Here and in Fig. 2, black circles and broken lines refer to plots dominated by alien species; solid lines, to reference plots.

log 10 of the number of trunks

Fig. 2. Logarithmic rank–abundance diagrams for species recorded in the tree and shrub layers of riparian forests in plots dominated by (a) *Robinia pseudoacacia*, (b) *Acer negundo*, or (c) *Amorpha fruticosa* and in reference plots dominated by native species.

cies were lower than in reference plots (Table 2). Consequently, species comprising the shrub layer in invaded plots were characterized by lower average abundance than species of corresponding ranks in reference plots dominated by native species. The diagram of the rank–abundance ratio for invaded plots is steeper than that for reference plots (Fig. 2), with the pattern of species abundance distribution being in good agreement with the geometric model in both groups of plots (Table 3).

The results of comparing the observed and hypothetically possible consequences of replacement of native by alien dominants (see Introduction) can be summarized as follows:

(1) Areas of forest phytocenoses dominated by *Ailanthus altissima* still contain a relatively large proportion of the former native dominant (*Alnus glutinosa*) and, therefore, are characterized by a lower dominance level, compared to reference communities (Table 4). Thus, they can be regarded as an example of the situation where the enrichment of the community species pool by alien species capable to reach high abundance leads to an increase in the number of potential dominants and a decrease in their individual relative abundance.

(2) The relative abundance of *Ficus carica* and *Robinia pseudoacacia* in the tree layer of forest phytocenoses is close to the relative abundance of native dominants in corresponding reference areas, and differences in species richness between the invaded and reference communities are also insignificant.

(3) The replacement of native by alien dominants (*Acer negundo* and *Amorpha fruticosa*) in the tree layer of riparian forests along the Pshish River and in the
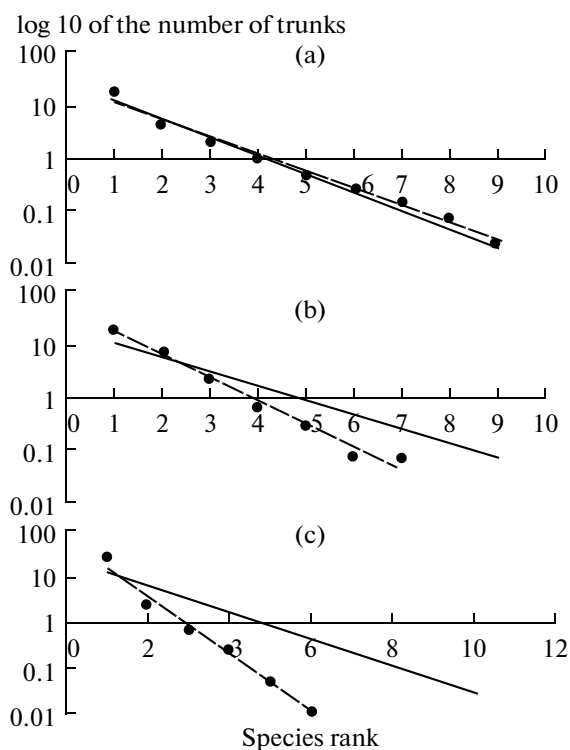
shrub layer of forests in the Belaya River valley has resulted in higher level of dominance and reduced species richness of these communities.

(4) Considering the structure of species abundance in the invaded and reference communities, attention should be given to two aspects: (1) in most cases, it well conforms to the geometric model; i.e., the replacement of native by adventive dominants has not altered the general pattern of resource distribution among species; and (2) in phytocenoses where adventive dominants have higher relative abundance than native dominants, the plot of the rank–abundance ratio is steeper than that for reference communities (parameter b has lower values; see Table 3). The first observation supports the assumption that the relative abundance of species of a certain rank is not incidental but reflects the general pattern of resource distribution. The second observation indicates that when an alien dominant becomes more abundant than the former native dominant of a given community (as observed for *Acer negundo* and *Amorpha fruticosa*), other species of this community (in order of their ranks) begin to utilize greater proportions of available resources, but the absolute density of these plants decreases.

The second observation can be correctly interpreted only if we know the mechanism forming the pattern of species abundance corresponding to the geometric

model. In particular, the formation of this pattern has been usually explained in terms of the aforementioned niche pre-emption hypothesis (Whittaker, 1980) or its subsequent stochastic variant named the dominance pre-emption model, according to which every new species invading a community intercepts part resources available to the least abundant species, with this part being not fixed but randomly variable within the limits specified by the model (Ferreira and Petrere, 2008). Some authors have noted that the geometric distribution of species abundance is observed in the communities where a single resource is utilized and the demands of species for this resource are distributed linearly (Puzachenko, 2006; Levich, 2007).

The geometric pattern of species abundance distribution may also result from the existence of positive feedbacks in the community, where more competitive species exceed others in abundance not only due to specific bioecological features allowing them to occupy the best biotopes and utilize more resources, but also because high abundance itself is a factor promoting its further increase. This phenomenon as a mechanism of dominance formation in plant communities was previously noted by Vasilevich (1991).

Unfortunately, the hypotheses considered above do not give unambiguous answers to the questions as to whether it is environmental conditions, the size of the species pool, or bioecological features of dominant species that determine the proportion of resources they utilize, and what factors account for the relationship between the proportions of resources utilized by the dominant and the species of all subsequent ranks. In such a situation, it is difficult to correctly understand the behavior of alien species under novel conditions and of native species in response to the replacement of dominants.

The results of our studies allow some tentative conclusions in this respect. First, the relative abundance of dominant species appears to be largely determined by their bioecological features and the actual situation in a given community. Second, the level of dominance of the strongest competitor has an effect on the proportions of remaining resources that can be utilized by accessory species of different ranks. Third, it appears most probable that the point is in the response of these species to the reduction of resources available to them: competition for resources becomes more severe, and the competitive advantage of one species over others is manifested more strongly.

Thus, the level of dominance in plant communities can theoretically be determined by different factors, and our results confirm that alien dominants do not necessarily achieve higher levels of relative abundance, compared to native dominants. But if they do, the species richness of communities decreases, because alien dominants as stronger competitors not only intercept a greater proportion of resources, compared to native dominants, but also provoke increasingly strict partitioning of remaining resources among associated species. In this context, the replacement of native by alien dominants in plant communities can be regarded as a factor placing them at high risk for reduction of species richness.

ACKNOWLEDGMENTS

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