

INVASIBILITY AND SPECIES RICHNESS OF A COMMUNITY: A NEUTRAL MODEL AND A SURVEY OF PUBLISHED DATA

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Abstract. A widespread but controversial idea in ecology states that the number of invaders of a species assemblage depends on its species richness. Both negative and positive relationships have been reported. We examined whether a simple neutral model where assemblages are generated by drawing individuals from two pools of identical species (native and alien) can predict this relationship. We performed a meta-analysis of published data on this relationship.

The neutral model showed that in communities with low and fixed numbers of individuals, the relationship between the number of aliens and native species is strong and negative. This becomes weaker as the proportion of species from both pools already present in the community increases. The relationship between alien and native species richness becomes positive when the number of individuals is allowed to vary, because the richness depends on number of individuals and/or area sampled. The meta-analysis showed that scale-dependence of the relationship between alien and native species richness is universal and compatible with the neutral model. Unless more evidence is available to refute it, the relationship between native and alien species richness should be considered a result of a neutral processes due to constraints on the number of individuals in the community.

Key words: *alien species; disturbance rate; meta-analysis; neutral process; scale; species-area relationship; species richness; transient dynamics.*

INTRODUCTION

Biological invasions, i.e., cases when an alien species increases and spreads in a new region, are of enormous practical interest (Elton 1958, Groves 1989, Levin 1989). However, understanding why a particular species establishes in a particular community can also shed light on the ecological processes structuring a community (Elton 1958, Shea and Chesson 2002), such as competition (Case 1996, Law and Morton 1996), disturbance (Fox and Fox 1986, Mooney and Drake 1986, Burke and Grime 1996), fluctuating resources (Davis et al. 2000), or growth rate ranking of species (Rejmánek and Richardson 1996).

One of the widespread but controversial ideas in ecology says that the number of alien species establishing in a community (community invasibility) is a function of the species richness of that community (Lonsdale 1999). Apart from experimental studies of invasion resistance, this has been studied by examining the relationship between the number of native and the number of alien species (slope of the native–alien relationship, further abbreviated NAR). While this approach has been criticized on methodological grounds

(Moore et al. 2001), it remains a widely used technique to assess community invasibility (Levine et al. 2002).

Several studies have reported NAR to be negative (Elton 1958, Lodge 1993), which is interpreted as an indication that more species-rich communities are more resistant to invasion. A negative NAR has been explained by the way niche space is filled by native species: If there are fewer native species, it is more likely that some regions of the niche space are empty and open for an invader (Case 1990, 1996, Law and Morton 1996, Prieur-Richard and Lavorel 2000, Shea and Chesson 2002). Other studies have reported NAR to be positive, which would indicate that species-rich communities are actually invaded by more alien species than communities that are species-poor (Pickard 1984, Lonsdale 1999, Pyšek et al. 2002, Sax 2002, Stohlgren et al. 2002); these studies are typically based on much larger sampling units such as islands or nature reserves. Several authors suggest that studies reporting a negative relationship are often experimental, whereas a positive relationship has been shown primarily by large-scale observational studies (Levine 2000, Naeem et al. 2000, Levine et al. 2002).

It is often assumed this inconsistency in NAR to be an artifact of scale (Moore et al. 2001, Levine et al. 2002). Shea and Chesson (2002) hypothesized that the negative NAR is found at any specific (sufficiently narrow) scale because of the effects of species interactions

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such as competition for resources or enemy-free space. Moore et al. (2001) showed that the sign and strength of NAR depends on the underlying cause of species richness, with negative slopes likely but by no means necessary. However, because the number of species depends on the size of the species assemblage, larger assemblages are bound to have more invaders simply due to the species-area relation (Shea and Chesson 2002). Thus, any sample that spans large and small assemblages should show a positive NAR even if the relationship at each specific scale may be negative. Indeed, Brown and Peet (2003) found that increasing the scale of the study changed NAR from negative or absent to positive (riparian communities in the eastern United States). Scale dependence may also arise as the amount or number of available resources changes with increasing scale (Byers and Noonburg 2003).

While such explanations are entirely feasible, it may not be necessary to assume any specific structure of interactions among species; it should first be examined to what extent patterns of NAR can be due purely to neutral processes operating over different scales. Simple neutral models are known to be able to account for many patterns found in species assemblages (Bartha and Ittzs 2001, Hubbell 2001); in particular, such models are often very successful in predicting changes in patterns at different scales.

In this paper, we compiled published data on NAR in plant species assemblages and performed a meta-analysis to test whether the NAR is indeed universally scale dependent. Furthermore, we tested whether a completely neutral model with no specific assumptions about the division of the niche space or competitive structure could generate NAR patterns similar to those found in the field data. We used a simple numerical simulation model of invasion dynamics for a community in which all species (both native and invaders) are completely identical, with only the immigration probabilities different, and recruitment occurs using a neutral lottery (see Sale 1977). In the model, there were two kinds of species pools: the species pool of native species and the alien species pool (invaders). The only differences between native and alien species were that no aliens were allowed in the initial species composition of the community and aliens could have different immigration probabilities. The scale effects were modeled by varying the number of individuals in the community over two orders of magnitude. We used this model to determine: (1) the expected relationship between the number of native species and the number of alien species (NAR) in the community from a neutral model, whether NAR depends on the community size (total number of individuals), and whether NAR changes when communities of different sizes are compared; (2) how NAR changes with the size of the species pools from which the community is drawn; (3) how NAR changes between transient (with a nonequilibrium number of invaders) and stable (with an equilibrium number

of invaders) states of the community. Comparison of transient and equilibrium states is motivated by the fact that most communities are likely not to have the equilibrium number of aliens.

METHODS

Analysis of published data

Data from all papers known to us reporting data on NAR in plants were collected (Table 1). We excluded papers that reported invasibility if the invasibility was measured by other criteria than the number of alien species present in the community (for example, resistance to invasion by one or several specific aliens); as a result, only one experimental study was included (Tilman 1997) with a sufficiently high pool of species (54) available as invaders. From all published data we extracted the following information:

1) Slope of the regression line of number of alien species on number of native species (NAR). Slopes were classified into three categories: significantly negative, significantly positive, and nonsignificant. Significance level of $\alpha = 0.05$ was used to assess significance. Because the individual data sets differed in the number of cases, power of the test was not the same across the data sets. If no regression was reported by the authors, but primary data on relationship between number of alien and native species per plot were available (Crawley 1986, Kruger et al. 1989, Vitousek et al. 1997, Mahelka et al. 2002), we reanalyzed them using Type I linear regression of number of aliens on number of native species. Further, we used our own unpublished data (K. Bímová and B. Mandák, *unpublished data*; B. Mandák, *unpublished data*).

2) Mean size (area) of study plots. If this was not available, the area was estimated indirectly from the information on the sampling protocol and community type (in the following papers: Kruger et al. 1989, MacDonald et al. 1989, Lonsdale 1999, Levine and D'Antonio 1999).

3) Range of plot sizes, calculated as difference in area between the largest and smallest study plots.

Differences between groups were tested using the Kruskal-Wallis criterion; significance was assessed using a Monte Carlo randomization based on 10 000 sampled tables. These statistical analyses were done using SPSS (SPSS 2002).

A subset of studies from which full primary data on number of aliens, number of native species, and area could be obtained (either numbers were directly available to us or could be measured on published plots) were used for a meta-analysis at the level of individual study units (plots, islands, reserves, etc.). Study unit sizes ranged from 1 m² to continents. Fifteen such studies (Table 1) were collected and all their data points (altogether 1172) were pooled. These data were used to fit and test a linear model with number of alien species as a dependent variable, and number of native

TABLE 1. Published data sets used in the meta-analysis.

Source	Sign of the NAR relationship	N	Mean area of one habitat (km ²)	Primary data used for meta-analysis?	Community type
K. Bímová and B. Mandák (<i>unpublished data</i>)	+	6	0.0000377	yes	riparian
Brown and Peet (2003)	+	107	0.0001	no	riparian
Brown and Peet (2003)	no	107	0.00001	no	riparian
Brown and Peet (2003)	no	107	0.000001	no	riparian
Brown and Peet (2003)	+	107	0.0000001	no	riparian
Brown and Peet (2003)	+	107	0.00000001	no	riparian
Crawley (1986)	+	13	3713.9	yes	smaller continental areas
Cully et al. (2003)	no	25	0.0697674	yes	tallgrass prairie
Fox and Fox (1986)	+	14	10	no	shrubland
Fox and Fox (1986)	no	16	10	no	healthland
Fox and Fox (1986)	no	9	10	no	islands
Hector et al. (2001)	-	80	0.000004	yes	grasslands
Kennedy et al. (2002)	-	174	0.000005	no	grasslands
Knops et al. (1995)	+	8	9.12†	no	different vegetation types
Kolb et al. (2002)	-	?	0.00000025	no	grasslands-coastal prairie
Kruger et al. (1989)	+	16	55†	no	smaller continental areas
Kruger et al. (1989)	+	4	55†	no	smaller continental areas
Kruger et al. (1989)	+	14	55†	no	smaller continental areas
Levine (2000)	-	65	0.000000035	no	riparian
Lonsdale (1999)	+	177	55†	yes	smaller continental areas (reserves)
MacDonald et al. (1989)	+	6	55†	no	forests (reserves)
MacDonald et al. (1989)	+	4	55†	no	forests (reserves)
Mahelka et al. (2002)	+	19	0.005779	yes	villages
Mandák (<i>unpublished data</i>)	+	97	0.0000103	yes	ruderal
McIntyre and Lavorel (1994)	-	120	0.00003	no	grasslands
Morgan (1998)	-	110	0.000001	yes	grasslands
Pickard (1984)	+	138	0.21	no	Lord Howe Island
Planty-Tabachhi et al. (1996)	+	32	1†	no	riparian
Planty-Tabacchi et al. (1996)	+	11	1†	no	riparian
Pyšek et al. (2002)	+	302	1.208	yes	smaller continental areas (reserves)
Sax (2002)	+	41	0.0004	yes	coastal sage scrub
Sax (2002)	+	20	0.0004	yes	xeric matorral
Sax (2002)	+	41	0.0001	yes	coastal sage scrub
Sax (2002)	+	20	0.0001	yes	xeric matorral
Sax (2002)	+	20	0.000025	no	xeric matorral
Sax (2002)	no	20	0.000001	no	xeric matorral
Smith and Knapp (1999)	+	115	0.00001	yes	ungrazed plots
Smith and Knapp (1999)	+	61	0.00001	yes	grazed plots
Stadler et al. (2000)	+	20	7146.75	yes	different community types
Stohlgren et al. (1999)	-	160	0.000001	yes	prairies
Stohlgren et al. (1999)	+	170	0.000001	yes	forests and grasslands
Stohlgren et al. (1999)	no	16	0.001	yes	prairies
Stohlgren et al. (1999)	+	17	0.001	yes	forests and grasslands
Stohlgren et al. (1999)	+	100	0.001	yes	grassland, riparian, and mountain
Tilman (1997)	-	30	0.00000025	no	grasslands
Timmins and Williams (1991)	no	234	10	no	reserves
Vitousek et al. (1997)	+	11	6 541 202	yes	large continental areas
Vitousek et al. (1997)	+	44	441 816.9	yes	smaller continental areas
Vitousek et al. (1997)	+	33	41 662.4	yes	islands

Notes: Slope of the regression line of number of alien species on number of native species (NAR): -, significantly negative; +, significantly positive; and no, nonsignificant. A significance level of $\alpha = 0.05$ was used. Sample size, N, is the number of units in each study.

† Value is estimated.

‡ Only data for which plot sizes could be extracted.

species, log of the plot size, and their interaction as predictors. Separate analyses were performed with untransformed and log-transformed numbers of species. While log-transformation was a more suitable method as numbers of species spanned several orders of mag-

nitude, analysis of untransformed data was also done to conform to the common approach used in most NAR studies. As the results were not qualitatively different, only log-transformed analyses are reported here. Code of the study or code of the data set within the study

(if it was identified as such by the author) were taken as cofactors to account for differences in species pools between studies. Significance of the interaction between plot size and number of native species indicates scale dependence of the relationship between number of native and alien species. Statistical analyses were done using S-Plus (Mathsoft 2000).

The simulation model

We built a simple dynamic simulation model of community invasion with all species (both native and invaders) and all individuals being identical. The model assumes a "local community," which is a set of individuals whose species identity is known; these species are classified as either native or aliens. The local community has a fixed (integer) number of individuals (community size, N); due to this constraint, there is "competition for space" in the community. Three processes operate in the local community at each step: disturbance, local replacement, and immigration.

To model disturbance, dN individuals are randomly removed from the local community at each step ($0 < d < 1$); each individual has equal probability to be removed irrespective which species it belongs to. Fractional numbers of individuals are rounded to the nearest integer.

The individuals removed by disturbance are then replaced by the following two processes. First, local replacement, i.e., the multiplication of species already present in the local community that survived the disturbance event, is simulated by drawing $l dN$ individuals from species already present in the community ($0 < l < 1$). The probability of drawing an individual from a species is a linear function of frequency of that species; probability of an individual of that the i th species being drawn thus equals

$$\frac{N_i}{\sum N_j}$$

where N_i is the number of individuals of the i th species in the community *after* the disturbance event; the summation is done over all species in the local community ("neutral lottery" of Sale 1977). These individuals can be either from the native or alien species pools provided they were present in the community after the disturbance ($N_i > 0$). Species not present in the community have zero probability to be drawn.

The remaining individuals, i.e., $(1 - l)dN$ individuals, are replaced by immigration from the outside of the community, both from the native species pool and the alien species pool. The probability of an individual of the i th species being drawn is

$$\frac{m_i}{P_{\text{native}} + m_{\text{alien}} P_{\text{alien}}}$$

where m_{alien} is the relative immigration rate of alien species (relative to immigration rates of native species

which are set to 1 without loss of generality), and P_{native} and P_{alien} are sizes of native and alien species pools. For alien species, $m_i = m_{\text{alien}}$, and $m_i = 1$ for native species. No account is taken whether the migrating species is already present in the community. Individuals are drawn from the species pools with replacement (i.e., species that have been drawn are available for drawing; several individuals may thus be drawn from one species). This process thus determines abundance distribution of species in each of the pools. Experiments with other abundance distributions, i.e., using different m_{alien} and m_{native} for individual species, showed that the choice of one particular abundance distribution does not qualitatively affect the result (data not shown here). There is no difference between species coming from the pool of native species and those from the pool of aliens, except that alien and native species may have a different rate of immigration into the local community ($m_{\text{alien}} \neq 1$) and sizes of the pools may be different ($P_{\text{native}} \neq P_{\text{alien}}$).

At step 0, both species pool of native species and species pool of aliens of given sizes and immigration rates are defined. Then a new local community is initialized by drawing all N individuals of the local community from the species pool of native species only; the probability of an individual of the i th species being drawn is thus $1/P_{\text{native}}$. Drawing is again done with replacement. Beginning with step 1, individuals of alien species were allowed to be drawn by immigration and local replacement in the same manner as were native species.

As a result of these processes, species richness and abundance in the local community reflect identical rules of disturbance, immigration, and ecological drift (stochastic variation due to low numbers) and the initial conditions (no alien species being present). This model uses reasoning similar to that of lottery models (Chesson and Warner 1981, Snyder and Chesson 2003), except that abundance in the pool does not influence the probability of recruitment. For obvious reasons, the number of species cannot exceed number of individuals in the local community; in most simulations species richness is, however, much smaller (depending on the size of the species pools relative to the community size). If the identical parameter combination is run in many realizations, the number of alien species may be regressed against the number of native species and the intensity of NAR measured.

Simulation experiments

We used this simulation model to investigate:

1) The effect of community size (N) and disturbance rate (d) on NAR. Communities of 20, 50, 100, 200, 500, 1000, and 2000 individuals were simulated. Simulations were run for species pools of 500 native species and 10 000 alien species, and native species had probability to arrive hundred times higher than alien species ($m_{\text{alien}} = 0.01$). Larger species pool and lower

immigration probabilities of alien species were used to mimic field conditions where local species pools are usually limited, but there are likely to be many more species potentially available for colonization from geographically distant habitats in same climatic zone. However, simulations with both identical species pools and identical immigration probabilities showed that the effects were not qualitatively different. Local replacement rate (l) was 0.5; disturbance rate (d) varied (0.1, 0.2, 0.3... up to 0.9 of the individuals removed at each step).

2) Effect of variation in community size (number of individuals) on NAR. Simulations were run for species pools of 500 native species and 10 000 alien species, and $m_{\text{alien}} = 0.01$. Number of individuals in the community was different in each realization (but held constant within the realization). Number of individuals was sampled from a uniform distribution with a lower limits of 50 individuals, and upper limits 100, 200, 500, 1000, and 2000 individuals. Local replacement rate (l) and disturbance rate (d) were 0.5.

3) Effects of varying sizes of species pools and immigration probabilities on NAR. Two separate experiments were performed. In the first experiment, the species pool of alien species was kept constant (10 000 species), and the species pool of native species was allowed to vary (200, 500, 1000, 2000, 5000, and 10 000). Immigration rate of native species was 100 times higher than that of alien species ($m_{\text{alien}} = 0.01$). In the latter experiment, the species pool size of native and alien species were identical (200, 500, 1000, 2000, 5000, and 10 000); immigration rates of both alien and native species were identical ($m_{\text{alien}} = 1$). Number of individuals in the community varied from 20 to 5000 individuals in all simulations. Local replacement rate (l) and disturbance rate (d) were 0.5.

These parameter choices were based on values tested in preliminary simulations (both species pools 100–20 000 species; local replacement rate from 0.1 to 0.9; disturbance rate from 0.1 to 0.9; m_{alien} from 1 to 0.001), which showed that settings of these parameters do not qualitatively affect the outcome of the simulation. Preliminary simulation experiments also showed that the number of invaders in the community reaches equilibrium by step 300 even for the lowest disturbance and highest local replacement regime. Therefore, we ran most of the simulations for 500 steps to get information on the equilibrium state; simulations run for five steps were used to get information on transients. Five hundred realizations of each parameter combination were run.

At the end of each simulation, the numbers of native and alien species were counted, and the sign of NAR (negative or positive) was determined over all realizations for that parameter combination. The strength of NAR was measured by the coefficient of determination (R^2) between the number of native and number

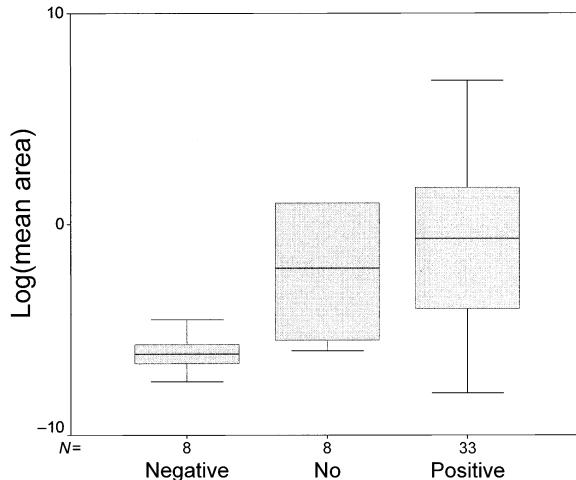


FIG. 1. Box-and-whisker plot of decadic logarithm of mean study area (originally measured in km^2 before log-transformation) of published studies reporting significant and negative, nonsignificant ("No"), and significant and positive relationships between number of aliens and number of native species (NAR). Boxes cover interquartile range, while whiskers indicate total range. N = number of cases in each category.

of alien species; R^2 was calculated over all realizations of each parameter combination.

RESULTS

Field data

Review of the published data showed that the pattern of scale dependence of NAR is a universal phenomenon. No study with a mean area of the plot larger than 30 m^2 reported a significant negative relationship between the number of alien and local species. Studies that reported positive or nonsignificant NAR were generally done at much larger plots/areas (Fig. 1). The difference is highly significant using a Kruskal-Wallis test ($\chi^2 = 14.07$, $df = 2$, $P < 0.001$ with nonsignificant relationships included; $\chi^2 = 13.15$, $df = 1$, $P < 0.001$ with nonsignificant relationships excluded). Nonsignificant relationships were found at plot sizes close to those of positive relationships; the difference is not significant ($\chi^2 = 0.88$, $df = 1$, $P = 0.357$).

In the subset of studies, areas of the smallest and largest unit covered by the data set were available in addition to the mean values ($n = 10$; studies done at plots of identical sizes were excluded). In these studies, there was a strong linear relationship between log of range (size difference between the smallest and largest unit) and log of mean ($R^2 = 0.944$).

Meta-analysis of published data from 15 studies showed a highly significant interaction between number of native species and $\log(\text{area})$ in the effect on the number of alien species (Table 2, Fig. 2). The effect was consistent no matter whether study or data set was taken as a cofactor (Table 2), or whether numbers of

TABLE 2. Meta-analysis of the published data on the relationship between number of native and alien species (NAR).

Effect	df	Study as cofactor		Data set as cofactor	
		F	P	F	P
Study	14	346.5	<0.001
Data set	36	188.7	<0.001
Log(native species)	1	574.1	<0.001	566.2	<0.001
Log(area)	1	0.0	0.94	2.2	0.14
Log (native species) × log (area)	1	36.2	<0.001	78.1	<0.001

Notes: The number of alien species (after log-transformation) is the dependent variable. Residual df = 1154 when study is taken as cofactor; df = 1132 when data set is taken as cofactor.

species (both native and alien) were untransformed or log-transformed (data not shown). Total species richness (native and alien) in the whole data set depends significantly on the area size with exponent of 0.204 ($R^2 = 0.840$).

Simulation experiments

Proportion of alien species increased rapidly over time in all the simulations; the slowest increase over time was in communities with low disturbance and high local replacement. While in the transient phase the number of alien species was strongly dependent on the disturbance rate, at equilibrium it stabilized at a level that was almost independent of the disturbance level (Fig. 3).

Simulations showed a strong effect of the number of individuals in the community on NAR. While for any fixed number of individuals the sign of NAR was negative, its intensity strongly varied as a function of spe-

cies pool size and number of individuals in the community. In communities with low number of individuals the correlation was very strong, with R^2 approaching 0.9 (Tables 3 and 4). In larger communities it became weaker; the decrease was slower when species pools were larger and local communities contained smaller proportion of the candidate species (Table 4). The strength of correlation between the number of aliens and number of native species depended on the proportion of the total species pools represented in the community; for the same number of individuals in the community, it decreased as the proportion of species represented in the community approached unity, either by one or both species pools (Table 4).

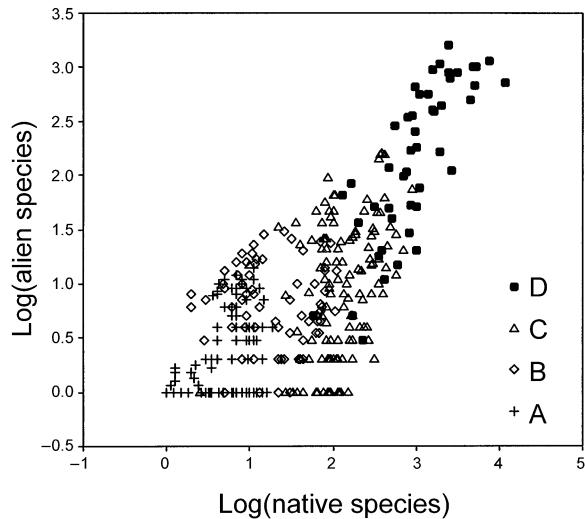


FIG. 2. Scale dependence of the relationship between the decadic log of number of native species and decadic log of number of alien species: A, plots $\leq 1 \text{ m}^2$; B, plots $1\text{--}300 \text{ m}^2$; C, plots $300 \text{ m}^2\text{--}10 \text{ km}^2$; and D, plots $>10 \text{ km}^2$. To improve visibility, the graph is based only on 20% randomly drawn data points of the total set of 1172 data points.

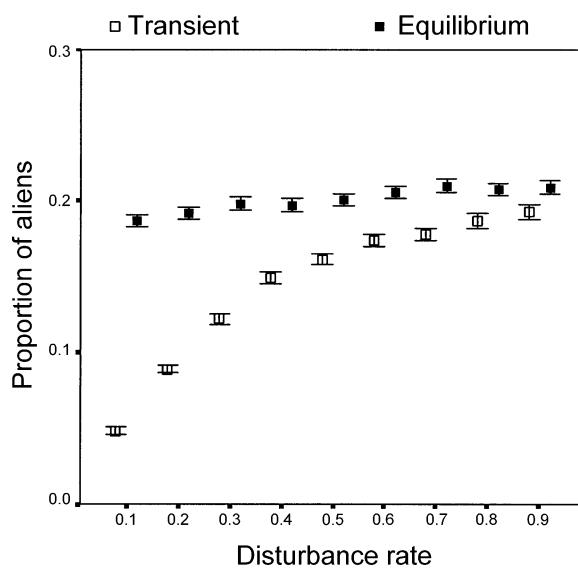


FIG. 3. Difference between the transient and equilibrium state in the effect of disturbance rate on the proportion of alien species (simulated data) (transient = step 5, equilibrium = step 500). Bars indicate 95% confidence intervals (based on 500 realizations of simulated data). Community size = 100 individuals, local replacement rate = 0.5; pool of alien species = 10 000, pool of native species = 500. All species are identical, except immigration rates of native species are 100 times higher than those of alien species.

TABLE 3. Relationship between number of alien species and number of native species (NAR, expressed as R^2 ; all relationships are negative) as a function of the local community size (simulated data).

No. individuals	Disturbance rate				
	0.1	0.3	0.5	0.7	0.9
20	0.300	0.504	0.651	0.708	0.898
50	0.416	0.458	0.529	0.664	0.810
100	0.308	0.431	0.452	0.522	0.703
200	0.338	0.265	0.364	0.452	0.600
500	0.250	0.184	0.229	0.324	0.478
1000	0.078	0.141	0.111	0.146	0.157
2000	0.029	0.068	0.045	0.058	0.122

Notes: Values are calculated from 500 realizations at equilibrium. Local replacement rate = 0.5; pool of alien species = 10 000, pool of native species = 500. All species are identical, except immigration rates of native species are 100 times higher than those of alien species.

As a result, if results of simulations with different numbers of individuals (sizes) were plotted together, a general positive relationship between number of local and alien species appeared, composed of negative relationships of different strengths for each specific community size (Fig. 4). When the number of individuals was allowed to vary in individual realizations, the shape of NAR varied as a function of the variation in the number of individuals, changing from negative through neutral to a positive relationship as the variation increased (Fig. 5).

The intensity of correlation between the number of aliens and number of native species was also affected by disturbance; at higher disturbance levels NAR was tighter (Table 3). The relationship changed only little from transient stage to equilibrium (data not shown) and is in the same range (for each community size)

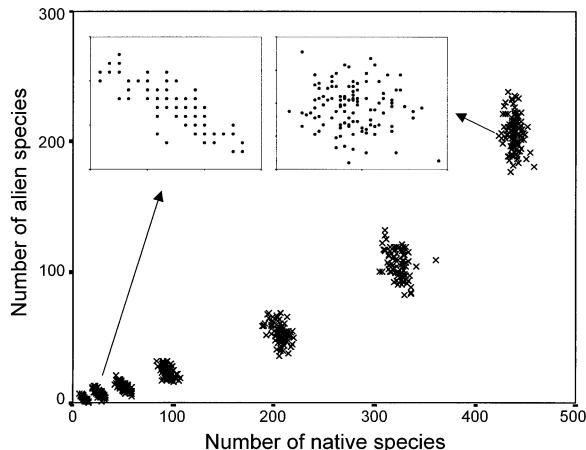


FIG. 4. Relationship between the number of alien species and number of native species at equilibrium over a range of community sizes (NAR; 100 realizations of simulated data for each community size). Individual point clusters correspond to communities of different sizes (numbers of individuals) ranging from 20 to 2000; inset plots are based on (left) communities of 50 individuals and (right) 2000 individuals only. Disturbance = 0.5, local replacement rate = 0.5; pool of alien species = 10 000, pool of native species = 500. All species are identical, except immigration rates of native species are 100 times higher than those of alien species.

both for transient and equilibrium communities. This contrasts with the systematic change in the proportion of alien species in the transient phase.

DISCUSSION

Neutral patterns in number of alien species

Published empirical data support the hypothesis that the scale dependence of the relationship between num-

TABLE 4. Coefficients of determination (R^2) between number of alien species and number of native species at equilibrium for communities of different source species pools (NAR; 500 realizations of simulated data for each community size).

Native pool	Alien pool	No. species								
		20	50	100	200	500	1000	2000	5000	No. individuals in the community
No. species in pool are equivalent										
200	200	0.106	0.520	0.523	0.355	0.225	0.083	0.050	0	
500	500	0.680	0.612	0.592	0.544	0.376	0.215	0.090	0.001	
1000	1000	0.732	0.686	0.611	0.614	0.488	0.374	0.234	0.053	
2000	2000	0.684	0.704	0.663	0.561	0.61	0.494	0.354	0.198	
5000	5000	0.715	0.691	0.669	0.623	0.651	0.586	0.585	0.347	
10000	10000	0.677	0.688	0.676	0.624	0.646	0.633	0.559	0.465	
No. species in pool differ										
200	10000	0.701	0.619	0.497	0.358	0.221	0.084	0.020	0	
500	10000	0.605	0.532	0.369	0.420	0.249	0.090	0.059	0	
1000	10000	0.482	0.414	0.316	0.311	0.256	0.067	0.048	0.021	
2000	10000	0.402	0.277	0.246	0.240	0.157	0.084	0.088	0.033	
5000	10000	0.276	0.268	0.169	0.145	0.111	0.084	0.078	0.030	

Notes: When pools differ (lower part of the table) immigration rates of native species are 100 times higher than those of alien species; otherwise immigration rates are identical. Disturbance = 0.5; local replacement rate = 0.5. The sign of the relationship was always negative.

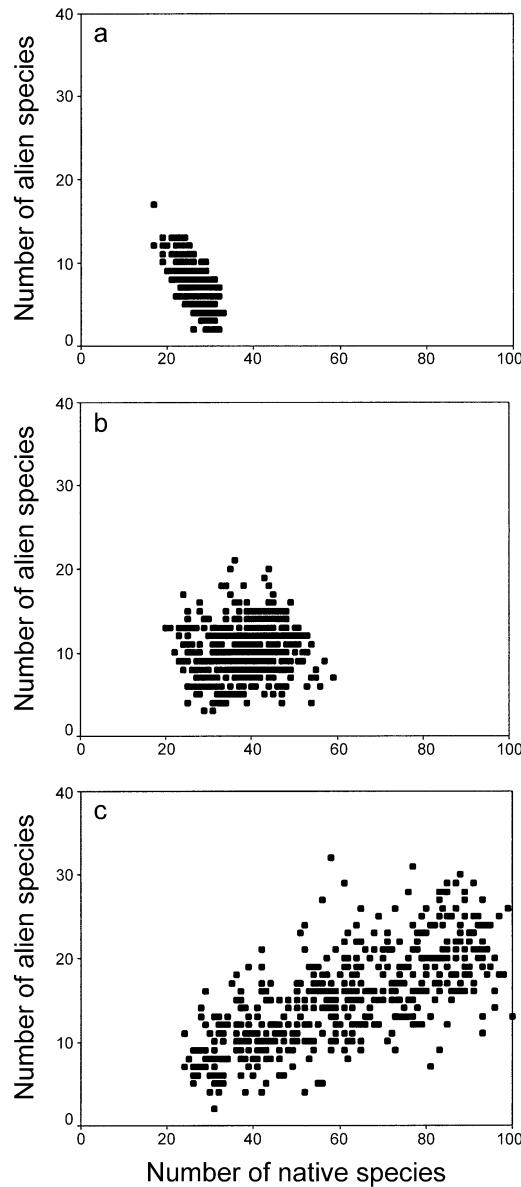


FIG. 5. Relationship between the number of alien species and number of native species at equilibrium for communities of different size variation (NAR; 500 realizations of simulated data for each community size): (a) number of individuals fixed at 50, (b) number of individuals sampled from the range 50–100, and (c) number of individuals sampled from the range 50–200. Disturbance = 0.5, local replacement rate = 0.5; pool of alien species = 10 000, pool of native species = 500. All species are identical, except immigration rates of native species are 100 times higher than those of alien species. Note that the same scaling is used in all three plots.

ber of aliens and number of native species (NAR) is quite universal. While there are a few exceptions, the overall pattern of negative NAR at small scales and positive or nonsignificant NAR at large scales is unlikely to be due to chance alone. Meta-analysis of the data showed a significant interaction between number

of native species and log(area) in the effect on the number of alien species, thus demonstrating that the relationship between number of alien and number of native species changes as a function of the study unit area.

The neutral model shows that no specific interaction structure of the communities needs to be assumed to explain the observed patterns of NAR; all its major features can be generated by a neutral process. If communities of same numbers of individuals are compared, the sign of NAR is always negative. This result is due to simple mathematics: Each individual can be either native or alien, but not both at the same time; if the number of individuals in the community is fixed and sufficiently small, a strong and negative relationship is inevitable. As the proportion of species from the species pool present in the community increases, NAR becomes weaker and essentially disappears. These patterns in NAR remain qualitatively the same over a range of values of other parameters, such as disturbance rate (Table 3), local replacement rate (data not shown here), or sizes of species pools (Table 4).

The neutral process produces strong and negative NAR only if numbers of (independent) individuals per community are small enough (below 200, depending on the species pool size). Data on numbers of individuals are thus necessary to assess whether the process could operate in the field (see also Oksanen 1996). A typical study reporting a negative NAR was done in grasslands at plots of 1 m² or smaller (Table 1); none of these studies report numbers of individuals. Published data on numbers of shoots per square meter in grasslands range over three orders of magnitude (for example, Klimeš [1995], 3357–3793 in grasslands; Zobel and Liira [1997], 164–16 546 in grasslands; Sandvik and Totland [2000], 15–337 in alpine communities; D. Goldberg [*unpublished data*], 59 to >13 000 in desert annuals). However, in most cases, plant shoots are not independent units due to ubiquitous clonal growth and resulting intraspecific spatial aggregation; therefore, the numbers of “independent” individuals are likely to be much lower. Assuming that an average tussock is composed of several tens of shoots, numbers of independent sampling units in a grassland may thus range around a few hundred per square meter. This may already be sufficient for neutral effects to play a role.

This neutral process operates independently whether the community is in equilibrium or not. This is important because it is likely that the number of aliens in any field community is not at equilibrium (Davis et al. 2000, Pyšek et al. 2002, Rejmánek 2003). However, intensity of disturbance does suppress the role of past events and local replacement; thus, it increases the intensity of NAR at small community sizes.

Variation in community size and number of alien species

The neutral process predicts a positive NAR only if the communities being compared are of different sizes

(numbers of individuals; see Fig. 5c), as also postulated by Shea and Chesson (2002). Positive NAR is a result of a stochastic process underlying general dependence of the number of species on number of individuals and/or area. This process is assumed to be one of the major factors accounting for the generality of the species-area relationship (He and Legendre 1996, 2002, Bartha and Ittzs 2001, Storch et al. 2003). The neutral model predicts the sign of NAR to depend on the range of the number of individuals in the study. The strength of the positive NAR increases as differences in community size increase. It should be noted that not only area itself, but also any factor that changes the number of individuals in the community would have the same effect. If communities of identical spatial extent but highly differing numbers of individuals (e.g., due to differences in productivity) are compared, the resulting relationship may still be positive.

The variation in community size is a critical difference between small- and large-scale studies. Small-scale studies are often done on plots of deliberately fixed sizes and thus no noticeable size variation (Tilman 1997, Stohlgren et al. 1999, Levine 2000), whereas observational data sets are often collected at larger physiographic units of variable sizes (Planty-Tabacchi et al. 1996, Lonsdale 1999, Pysek et al. 2002). Analysis of published data sets shows that the range of plot sizes systematically increases with the mean plot size, which is a universal phenomenon (e.g., McCullagh and Nelder 1989). The neutral model presented here thus predicts a negative NAR for small plots where there is little variation in size, while positive NAR for large plots with considerable variation in size. The difference in size and range can therefore explain the difference between experimental studies that find negative NAR and descriptive studies that find positive NAR: Since almost all the experimental studies are done at small scales, the simple difference in scale range might have lead to the conclusion that experimental approach leads to a different conclusion (Levine et al. 2002).

There may be an additional confounding effect of spatial heterogeneity at plots of larger sizes ("covarying factors" of Shea and Chesson 2002) as heterogeneity becomes more important as plot sizes increase. Therefore, even if large-scale studies are done at areas of fixed sizes (Brown and Peet 2003), plots that are more spatially heterogeneous are bound to bear more species, most likely both of native species and aliens, than plots that are more homogeneous, with a positive NAR again being the resulting effect (Levine et al. 2002).

The neutral model used also shows a strong effect of the size of the species pool relative to the number of species in the community (see Bartha and Ittzs 2001 for a discussion of the issue). As the proportion of species represented in local community approaches unity (i.e., number of *individuals* in the community is large relative to the number of *species* in the species

pool), the intensity of NAR decreases and it eventually disappears. If all candidate species are already present, NAR is bound to be exactly zero. The same effect accounts for the convex shape of NAR over several community sizes if alien and native species pool differ. When the species pool of aliens is larger (as it is likely to be, because of many more species being available in geographically distant habitats in same climatic zone than there are in the local species pool), at certain community sizes most species from the native species pool are already represented, while alien species are still available for immigration.

While the neutral patterns can be generated by a very simple model, both major mechanisms in the model, i.e., sampling from species pools and constraint on number of individuals are present in some form in all ecological systems. Of course their representation in the neutral model is simplistic, because in plant communities often total biomass and not the number of individuals is constrained (Harper 1977). Even without these simplifications, constraints similar to those shown by the neutral model are inevitable in any ecological system (for a discussion of similar processes, see Oksanen 1996, Pärtel and Zobel 1999, Zobel 2001). They are unlikely to be strongly modified by processes of, e.g., biotic interactions as such processes operate independently of the neutral constraints. Therefore, unless evidence is available to refute it, the patterns of relationship between number of native and alien species should be considered a result of a neutral process due to constraints on the number of individuals in the community and scale-dependent effects of species-area relationship.

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LITERATURE CITED

- Bartha, S., and P. Ittzs. 2001. Local richness-species pool ratio: a consequence of the species-area relationship. *Folia Geobotanica* **36**:9–23.
- Brown, R. L., and R. K. Peet. 2003. Diversity and invasibility of southern Appalachian plant communities. *Ecology* **84**: 32–39.
- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776–790.
- Byers, J. E., and E. G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. *Ecology* **84**:1428–1433.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences (USA)* **87**:9610–9614.
- Case, T. J. 1996. Global patterns in establishment of exotic birds. *Biological Conservation* **78**:69–96.

- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive-systems. *American Naturalist* **117**:923–943.
- Crawley, M. J. 1986. What makes a community invasible? Pages 429–453 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. *Colonization, succession and stability*. Blackwell Science, Oxford, UK.
- Cully, A. C., J. F. Cully, and R. D. Hiebert. 2003. Invasion of exotic plant species in tall grass prairie fragments. *Conservation Biology* **17**:990–998.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528–534.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57–66 in R. H. Groves and J. J. Burdon, editors. *Ecology of biological invasions, an Australian perspective*. Australian Academy of Science, Canberra, Australia.
- Groves, R. H. 1989. Ecological control of invasive terrestrial plants. Pages 437–461 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK.
- He, F. L., and P. Legendre. 1996. On species-area relations. *American Naturalist* **148**:719–737.
- He, F. L., and P. Legendre. 2002. Species diversity patterns derived from species-area models. *Ecology* **83**:1185–1198.
- Hector, A., K. Dobson, A. Minns, E. Bazeley-White, and J. H. Lawton. 2001. Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research* **16**: 819–831.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**:636–638.
- Klimeš, L., 1995. Small scale distribution of species richness in a grassland (Bílé Karpaty Mts., Czech Republic). *Folia Geobot. Phytotax.* **30**:499–510.
- Knops, J. M. H., J. R. Griffin, and A. C. Royalty. 1995. Introduced and native plants of the Hasting Reservation, central coastal California: a comparison. *Biological Conservation* **71**:115–123.
- Kolb, A., P. Alpert, D. Enters, and C. Holzapfel. 2002. Patterns of invasion within a grassland community. *Journal of Ecology* **90**:871–881.
- Kruger, F. J., G. J. Breytenbach, A. W. Macdonald, and D. M. Richardson. 1989. The characteristics of invaded Mediterranean-climate regions. Pages 181–213 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK.
- Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* **77**:762–775.
- Levin, S. A. 1989. Analysis of risk for invasions and control programs. Pages 425–435 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK.
- Levine, J. 2000. Species diversity and biological invasions: relating local process to community pattern. *Science* **288**: 852–854.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**:15–26.
- Levine, J. M., T. Kennedy, and S. Naeem. 2002. Neighborhood scale effects of species diversity on biological invasions and their relationship to community patterns. Pages 79–91 in M. Loreau, S. Naeem, and P. Inchausti, editors. *Biodiversity and ecosystem functioning: synthesis and perspectives*. Oxford University Press, Oxford, UK.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology and Evolution* **8**:133–137.
- Lonsdale, W. M. 1999. Global patterns of invasions and the concept of invasibility. *Ecology* **80**:1522–1536.
- MacDonald, I. A. W., L. L. Loope, M. B. Usher, and O. Hamann. 1989. Wildlife conservation and the invasion of nature reserves by introduced species: a global perspective. Pages 215–255 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, Chichester, UK.
- Mahelka, V., B. Mandák, and K. Bímová. 2002. Synanthrophic flora of selected villages in the Kokořínsko Protected Landscape Area. *Zprávy České Botanické Společnosti* **37**:171–183. [In Czech.]
- Mathsoft. 2000. S-Plus. Version 6. Mathsoft, Seattle, Washington, USA.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Chapman and Hall, London, UK.
- McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare and exotic plants in response to habitat and disturbance variable across a variegated landscape. *Conservation Biology* **8**:521–531.
- Mooney, H. A., and J. A. Drake, editors. 1986. *Ecology of biological invasions of North America and Hawaii*. Springer-Verlag, New York, New York, USA.
- Moore, J. L., N. Mouquet, J. H. Lawton, and M. Loreau. 2001. Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos* **94**:303–314.
- Morgan, J. W. 1998. Patterns of invasion of an urban area remnant of a species-rich grassland in southeastern Australia by non-native plant species. *Journal of Vegetation Science* **9**:181–190.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying factors. *Oikos* **91**:97–108.
- Oksanen, J. 1996. Is the humped relationship between species richness and biomass an artefact due to plot size? *Journal of Ecology* **84**:293–295.
- Pärtel, M., and M. Zobel. 1999. Small-scale plant species richness in calcareous grasslands determined by the species pool, community age and shoot density. *Ecography* **22**: 153–159.
- Pickard, J. 1984. Exotic plants on Lord Howe Island: distribution in time and space 1853–1981. *Journal of Biogeography* **11**:181–208.
- Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Defferrari, and H. Decamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* **10**: 598–607.
- Prieur-Richard, A. H., and S. Lavorel. 2000. Invasions: the perspective of diverse plant communities. *Australian Ecology* **25**:1–7.
- Pyšek, P., V. Jarošká, and T. Kučera. 2002. Patterns of invasion in temperate nature reserves. *Biological Conservation* **104**:13–24.
- Rejmánek, M. 2003. Patterns of non-native plant species richness in the United States: a comment. *Frontiers in Ecology and the Environment* **1**:122–123.

- Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**:1655–1661.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**:337–359.
- Sandvik, S. M., and O. Totland. 2000. Short-term effects of simulated environmental changes on phenology, reproduction, and growth in the late-flowering snowbed herb *Saxifraga stellaris* L. *Ecoscience* **7**:201–213.
- Sax, D. F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distribution* **8**:193–210.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* **17**:170–176.
- Smith, M. D., and A. K. Knapp. 1999. Exotic species in a C₄-dominated grassland: invasibility, disturbance, and community structure. *Oecologia* **120**:605–612.
- Snyder, R. E., and P. Chesson. 2003. Local dispersal can facilitate coexistence in the presence of permanent spatial heterogeneity. *Ecology Letters* **6**:301–309.
- SPSS. 2002. SPSS. Version 11.5.1. SPSS, Chicago, Illinois, USA.
- Stadler, J., A. Trefflich, S. Klotz, and R. Brandl. 2000. Exotic plant species invade diversity hot spots: the alien flora of northwestern Kenya. *Ecography* **23**:169–176.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25–46.
- Stohlgren, T. J., G. W. Chong, L. D. Schell, K. A. Rimar, Y. Otsuki, M. Lee, M. A. Kalkhan, and C. A. Villa. 2002. Assessing vulnerability to invasion by nonnative plant species at multiple spatial scales. *Environmental Management* **29**:566–577.
- Storch, D., A. L. Šízling, and K. J. Gaston. 2003. Geometry of the species-area relationship in central European birds: testing the mechanism. *Journal of Animal Ecology* **72**:509–519.
- Tilman, D. 1997. Community invasibility, recruitment limitation and grassland biodiversity. *Ecology* **78**:81–92.
- Timmins, S. M. and P. A. Williams. 1991. Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology* **15**:153–162.
- Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmánek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* **21**:1–16.
- Zobel, K. 2001. On the species-pool hypothesis and on the quasi-neutral concept of plant community diversity. *Folia Geobotanica* **36**:3–8.
- Zobel, K., and J. Liira. 1997. A scale-independent approach to the richness vs biomass relationship in ground-layer plant communities. *Oikos* **80**:325–332.