

LETTER

Species pool size and invasibility of island communities: a null model of sampling effects

Tomáš Herben

Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice; and Department of Botany, Faculty of Science, Charles University, Benátská 2, CZ-128 01 Praha 2, Czech Republic

Correspondence: E-mail: herben@site.cas.cz

Abstract

The success of alien species on oceanic islands is considered to be one of the classic observed patterns in ecology. Explanations for this pattern are based on lower species richness on islands and the lower resistance of species-poor communities to invaders, but this argument needs re-examination. The important difference between islands and mainland is in the size of species pools, not in local species richness; invasibility of islands should therefore be addressed in terms of differences in species pools. Here I examine whether differences in species pools can affect invasibility in a lottery model with pools of identical native and exotic species. While in a neutral model with all species identical, invasibility does not depend on the species pool, a model with non-zero variation in population growth rates predicts higher invasibility of communities of smaller pools. This is because of species sampling; drawing species from larger pools increases the probability that an assemblage will include fast growing species. Such assemblages are more likely to exclude random invaders. This constitutes a mechanism through which smaller species pools (such as those of isolated islands) can directly underlie differences in invasibility.

Keywords

Alien species, population growth rate, species pool, species sorting.

Ecology Letters (2005) 8: 909–917

INTRODUCTION

The success of alien species on oceanic islands is considered one of the classic observed patterns in ecology (Lonsdale 1999; Sax 2001; Denslow 2003). This has been extensively documented for plants (Lonsdale 1999), birds (Case 1996, but see Sol 2000), as well as for other groups (Gaston *et al.* 2003). While many functional explanations of this phenomenon (e.g. introduction of herbivores, different fire regimes) have been proposed (Courchamp *et al.* 2003), most of the explanations attribute increased invasibility to lower species richness.

It has been suggested that species-poor communities show lower resistance to invaders (Lonsdale 1999; Sax 2001); because islands are generally more species-poor, their invasibility should be higher. However, a closer examination is necessary here. First, it is not fully clear whether species-rich communities are indeed less susceptible to invasion (Levine & D'Antonio 1999). Analysis of model communities often shows increased resistance to invasion in species-rich communities (Case 1990; Law & Morton 1996). However, Moore *et al.* (2001) showed in an elegant study that

resistance to invasion in model communities strongly depends on the mechanism that is assumed to maintain diversity in these communities; by changing this mechanism, both negative and positive relationships can be obtained. Field data show both positive and negative effects of species richness on invasibility (Naeem *et al.* 2000; Kennedy *et al.* 2002; Levine *et al.* 2002), and the relationship between native species richness and number of alien species is clearly scale-dependent (Fridley *et al.* 2004; Herben *et al.* 2004). It can be shown that if there is no constraint on community size and there is an underlying (statistical or biological) process that affects species richness, the same process that increases species richness of local species may also increase that of aliens (Levine *et al.* 2002; Shea & Chesson 2002).

Second, the lower species richness on islands is typically manifested by higher average slopes of the species–area relationships for islands (Rosenzweig 1995). Thus islands are more impoverished relative to mainland plots of the same size, presumably primarily because of restricted immigration to small and/or isolated islands (MacArthur & Wilson 1967). This means that islands, in particular small islands, have a smaller species pool. Species pool in this context is

the set of species whose propagules can reach the community in reasonable time and therefore have provided the species that occur in the given habitat (Zobel 1997). A steeper species–area relationship at the whole island level, however, does not necessarily mean differences in community richness at a smaller scale. The major difference between islands and continents is not difference in species richness per unit area, but the fact that an island community is a small sample from the set of potential species that can survive in a given set of habitat conditions.

Therefore, invasibility of islands should primarily be framed in terms of differences in species pools of native species, not of differences in local species richness. In a larger pool, the likelihood of finding a better adapted species or a better competitor for given set of conditions is higher (Huston 1997; Tilman *et al.* 1997). This issue has been extensively addressed in biodiversity studies ('chance' or 'sampling effect'; Lepš *et al.* 2001; Hector *et al.* 2002; Aarssen *et al.* 2003), but it has not been applied in the context of invasion ecology.

In this paper, I used a null model to test whether difference in the size of native species pools (as a consistent difference between islands and continents) can account for differences in invasibility, holding local (plot-level) richness constant. The model used here is a generalized version of that in Herben *et al.* (2004). It is a dynamic lottery model, based on drawing individuals from two pools of identical species (native and exotic), with lottery processes of disturbance and local growth (Sale 1977; Chave 2004). Species differences are modelled by different growth rates; the neutral lottery model with identical growth rates for all species (similar to that used by Hubbell 1979) is used as a reference to account for pure sampling effects. The model assumes a strict carrying capacity such that the total number of individuals in the community is fixed. Community structure is then determined by replacement probabilities of deceased individuals. Replacement probabilities are influenced by current species abundances, growth rates, and immigration rates. The only dynamic difference between native and alien species is that no aliens are allowed in the initial structuring of the native community, which is allowed to develop by random drawing of species from the native species pool for some time.

The model was used to examine the effect of the size of the native species pool on the number of species and individuals of aliens in the community; smaller pools of native species were used as a proxy for an island/continent contrast in the model. Each simulation run began with a period over which only native species were drawn from the species pool (to enable species sorting in the community under isolation); only later alien species were allowed to establish. This approach was then used to examine how invasibility is affected by the length of this period, by the

degree of variation in population growth rates, and by different disturbance and immigration rates.

METHODS

A 'local community' with a constant total number of individuals (community size, N) was constructed by random drawing from species pools with a simple dynamic simulation model of community invasion. The pool is a set of individuals whose species identity is known; these species may be either native or alien. Individuals of all species are identical except that species may differ in per-capita population growth rates.

First, species pools of native and alien species of given sizes and immigration rates are constructed. The only differences between species coming from the native species pool and those from the alien pool are in rates of immigration into the local community ($m_{\text{alien}} \neq m_{\text{native}}$) and sizes of species pools ($P_{\text{native}} \neq P_{\text{alien}}$). To prevent trivial effects of species pool size, the immigration probability summed over all species was kept constant by changing values of immigration rates according to the size of the respective species pool ($m_{\text{native}}P_{\text{native}} = \text{const.}$, and $m_{\text{alien}}P_{\text{alien}} = \text{const.}$). This means that a constant number of immigrant individuals are drawn independently of the size of each of the species pools. Per-capita population growth rate of each species (both native and alien) was drawn from a gamma distribution with a mean of 1 and a variation coefficient which is one of the model parameters (for the summary of model parameters, see Table 1). A gamma distribution was used to generate skewed distribution (McCullagh & Nelder 1989). Mean growth rate does not affect the model because only relative growth rates are important in a null model with a fixed community size. Identical variation in growth rates was used among species within both the native and alien species pools.

Next, a new local community is initialized by drawing N individuals from the species pool of native species; the probability of an individual of the i th species being drawn is thus $1/P_{\text{native}}$, where P_{native} is the size of native species pool. Drawing is done with replacement, i.e. several individuals may be drawn from one species.

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 an equal probability of being removed irrespective of species identity. Fractional numbers of individuals are rounded to the nearest integer. The individuals removed by disturbance are then replaced by local replacement and by immigration. Local replacement (i.e. population growth of species already present in the local community that survived the disturbance event) is simu-

Table 1 Parameters used by the simulation model

Parameter	Symbol	Values used
Community size (number of individuals)	N	500 , 2000
Number of species in the species pool of native species	P_{native}	100 , 1000 , 10000
Number of species in the species pool of aliens	P_{alien}	500 , 5000
Disturbance rate (number of individuals removed from the community at each step)	d	0.1 , 0.3, 0.5, 0.7
Proportion of local replacement (fraction of vacant positions filled by growth of species already present in the community)	l	0.2, 0.5 , 0.7, 0.9 , 0.99
Rate of immigration of native species into the local community*	m_{native}	0.5 , 0.05 , 0.005
Rate of immigration of alien species into the local community*	m_{alien}	0.1 , 0.01
Variation coefficient of species relative population growth rates	$\text{cv}(\hat{r})$	0, 0.05, 0.2, 0.5 , 0.7, 0.99
Number of steps before alien species are allowed to arrive		1 , 5 , 10 , 100 , 300
Number of steps after alien species are allowed to arrive		5 , 100

Default values (values used in most simulations) shown in boldface.

*Values changed together with the species pool size in order to keep the immigration probability summed over all species in the species pool constant.

lated by drawing $l d N$ individuals from species already present in the community ($0 < l < 1$). The probability of drawing an individual from species i is a function of frequency of that species and its population growth rate, $r_i N_i / (\sum_j r_j N_j)$, where N_i is the number of individuals of the i th species in the community after the disturbance event and r_i its (relative) population growth rate; the summation is done over all species in the local community. These individuals can be either native or alien provided they were present in the community prior to the disturbance ($N_i > 0$). Species not present in the community have zero probability of being drawn here.

The remaining $(1 - l) d N$ individuals are replaced by immigration from the outside of the community. Initially, only species from the native species pool can immigrate; the probability of an individual of the i th species being drawn is then $1/P_{\text{native}}$. After a specified number of steps (one of the model parameters), individuals of alien species can also immigrate; the probability of an individual of the i th species being drawn is then $m_i / (m_{\text{native}} P_{\text{native}} + m_{\text{alien}} P_{\text{alien}})$, where m_{native} and m_{alien} are relative immigration rates of native and alien species, respectively, P_{alien} the size of the alien species pool, and m_i equals m_{alien} or m_{native} for alien and native species, respectively. No account is taken of whether the species to which the individual drawn belongs is already present in the community. Individuals are drawn from the species pools with replacement (i.e. several individuals may be drawn from one species); this process determines the abundance distribution of species in the community.

As a result of these processes, the numbers of species present in the local community and their abundances reflect identical rules of disturbance, immigration, and ecological

drift (stochastic variation because of low numbers) under the constraints of varying population growth rates. The numbers of individuals and of alien species were recorded after five and 500 steps of invasion. In addition, abundance distribution data (both for native and alien species separately) were collected and summarized by Simpson's index of dominance concentration $[\sum_i (N_i/N)^2]$, where $N = \sum_i N_i$.

The simulation model was used to perform the following experiments: (i) a test of the effects of variation in population growth rate and native species pool size on the numbers of individuals and species of aliens (for the parameter values in Table 1); (ii) a test of the effects of length of native community development (or sorting) time before invasion and native species pool size on the numbers of individuals and species of aliens; (iii) a test of the effects of the proportion of replacement by local individuals and native species pool size on the numbers of individuals and species of aliens. In each experiment, 500 realizations of each parameter combination were run, and the means of these runs were compared over parameter values of interest.

The parameter values were chosen to cover likely meaningful values in the field (both species pools 100–100000 species; local replacement rate 0.1–0.99; disturbance rate 0.1–0.9; m_{alien} : 1–0.001, m_{native} : 1–0.001; community size 100–5000). These values were tested in preliminary simulations which showed that settings of the parameters do not qualitatively affect outcome of the simulation.

RESULTS

In a fully neutral model with no variation in population growth rates between species, the size of the local species

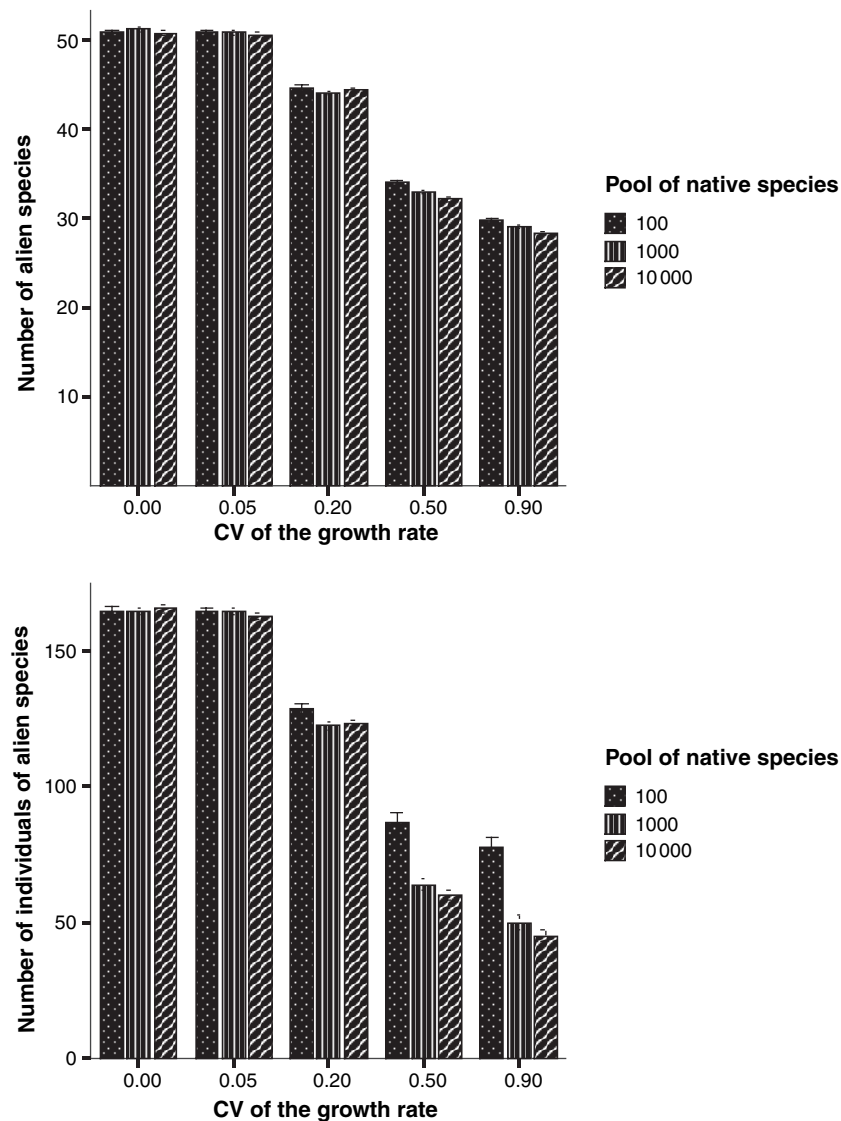


Figure 1 The effect of the size of the pool of native species and the CV of growth rate on the number of species and number of individuals of aliens. Other parameters: proportion of local replacement = 0.9; alien species pool = 500; number of individuals = 500; duration of invasion = 10 steps; number of steps before invasion began = 100. Bars indicate 1 SE.

pool did not affect the final number of species or number of individuals of aliens (Fig. 1, leftmost columns). In contrast, a model with a non-zero variation in population growth rates consistently predicted higher numbers of species and, particularly, numbers of individuals of aliens, if local species pools were small. The strength of the effect depended on the coefficient of variation of population growth rates (Fig. 1); the higher the coefficient, the larger the effect of species pool size on invasibility of island assemblages. The length of the period before the alien species were allowed to settle had an important effect as well; the longer the community had to sample from the native species pool, the greater was its resistance to invasion (Fig. 2). The strength of this effect depends on the proportion of local replacement (Fig. 3), attaining the greatest magnitude for intermediate values of local replacement. This relationship is

essentially scale-independent and appeared for any community size (number of individuals) studied (data not shown).

The richness of alien species was generally weakly negatively correlated with the richness of native species within each combination of parameter values (coefficients of determination varied between 0 and 0.56, depending on the parameter values; data not shown). In contrast, when simulation results using several values of any one parameter that affects species sorting (e.g. proportion of local replacement, size of local species pool, etc.) were analysed together, the correlation changed to positive in spite of identical community sizes (for an example, see Fig. 4). Increasing variation in population growth rates among species also causes abundance distribution curves to become steeper [median of the Simpson's index changes from 0.02 for the fully neutral model to 0.72 for the model with

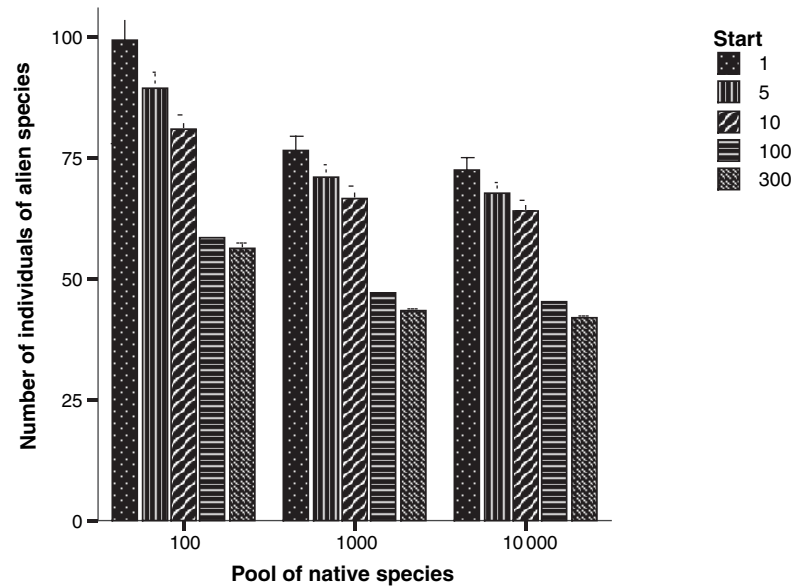
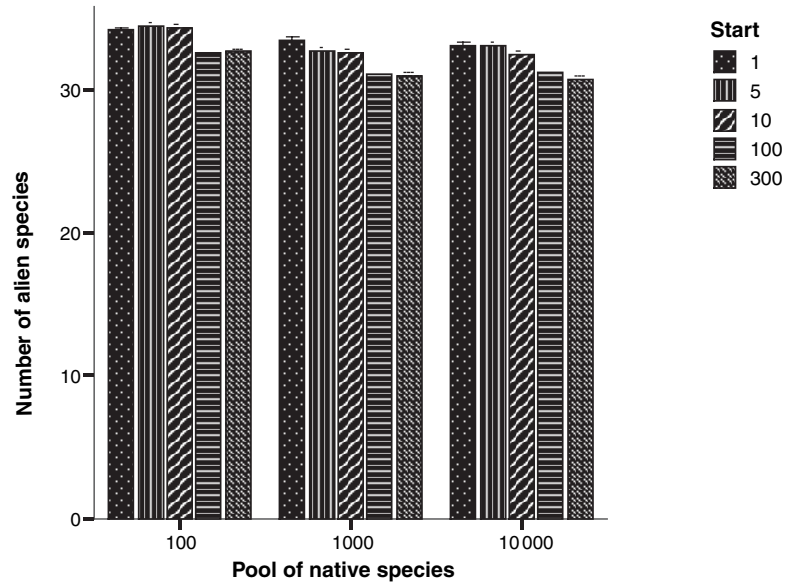


Figure 2 The effect of the size of the pool of native species and number of time steps before invasion on the number of species and number of individuals of aliens. Steps: number of time steps before species from the alien pool are allowed to establish. Other parameters: alien species pool = 500; number of individuals = 500; duration of invasion = 100 steps; variation coefficient of species population growth rates = 0.5; proportion of local replacement = 0.9.

$cv(r) = 0.99$]. Massive invasions were therefore more likely when the abundance distribution of the community was rather flat, with no major dominant (Fig. 5).

DISCUSSION

The simulations show that if variation in population growth rates is non-zero, no other process is needed to explain higher invasibility of communities with smaller pools of native species. This is because of the initial period of sampling of species from the native species pool combined with local replacement: species with higher population growth rates are more likely to survive and thus become dominant if dead individuals are replaced by growth of

species already present. If the period over which such sorting takes place is sufficiently long, the species pool is sampled thoroughly enough to produce a local community composed of 'good' (i.e. having high population growth rates) species. Such an assemblage is therefore much more likely to block establishment of a randomly drawn invader, because the invader's population growth rate is on average lower than that of most species already present in the community (because these already are a non-random sample because of the sorting). For the same reason, the invasibility decreases with the time period over which sampling from the local pool can take place: the longer the species pool is sampled, the more likely a community of faster growing species is obtained.

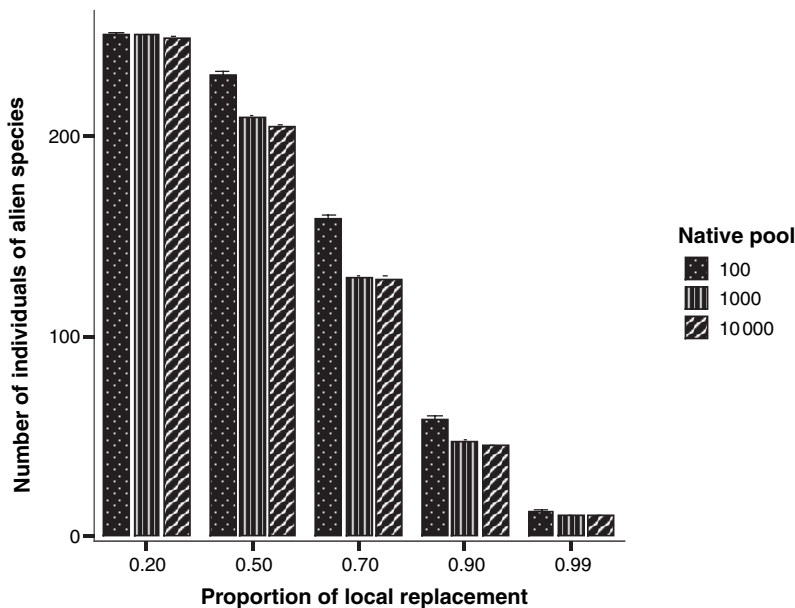


Figure 3 The effect of the size of the proportion of local replacement and the pool of native species on the number of individuals of aliens. Number of time steps before species from the alien pool are allowed to establish = 100; alien species pool = 500; number of individuals = 500; duration of invasion = 100 steps; variation coefficient of species population growth rates = 0.5. Bars indicate 1 SE.

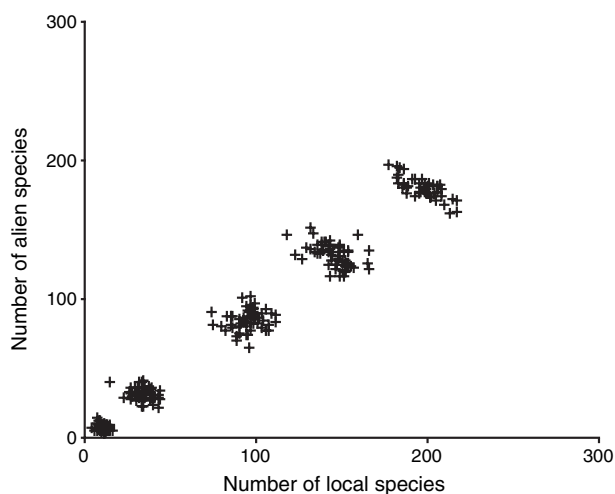


Figure 4 Relationship between the number of native species and the number of aliens over different proportions of local replacement (simulations with all values of this parameter are lumped together). Number of time steps before species from the alien pool are allowed to establish = 100; alien species pool = 500; number of individuals = 500; duration of invasion = 100 steps; variation coefficient of species population growth rates = 0.5; local species pool = 1000.

A similar effect (sampling effect) has been identified and extensively studied in biodiversity–productivity studies (Huston 1997; Tilman *et al.* 1997): species-rich communities are more likely to contain a highly successful species that drives ecosystem functions, such as productivity, irrespective of the effect of diversity per se. This process is identical to that operating in the present model. The sampling effect

has been shown to account for a large part of the effect of richness on productivity and other ecosystem functions (Lepš *et al.* 2001; Hector *et al.* 2002; Polley *et al.* 2003).

In the present context, species growth rates should be understood strictly in relative terms within the given environment: population growth rate is used here as a proxy for species performance in an environment, regardless of whether its success is because of competitive superiority, stress tolerance, or other mechanisms. The assumption of varying population growth rate makes it possible, in very general terms, to account for species sorting by environmental conditions and the realistic dominance hierarchies that exist among species in ecological systems.

The relationship between species pool size and invasibility has rarely been explicitly addressed. In an elegant study, Smith & Knapp (2001) showed that species pool does have a strong effect on invasibility; communities with larger species pools were less invasible. However, in most field studies, data are collected at only one scale, making the effects of species pool difficult to separate from species richness (see e.g. Pärtel *et al.* 1996; Grace 2001; Wilson & Anderson 2001). This is true both for data sampled at smaller scales, where only richness data are available without any information on species pools (e.g. Davis *et al.* 2000; Kennedy *et al.* 2002; Fargione *et al.* 2003), or large-scale data, which are generally collected on larger plots where species richness and species pool are difficult to distinguish (see e.g. Lonsdale 1999).

This null version of species sorting according to their population growth rates tends to produce communities with higher skew in their abundance distribution as they become dominated by a few highly successful (i.e. fast growing)

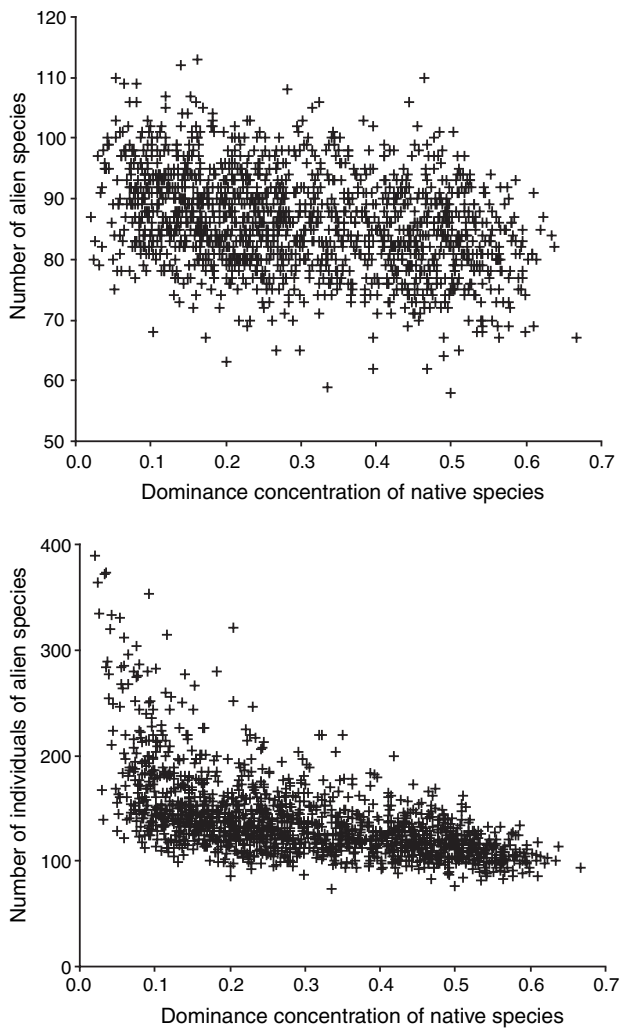


Figure 5 The effect of the size of the pool of native species on the number of individuals of aliens. Number of time steps before species from the alien pool are allowed to establish = 100; alien species pool = 500; number of individuals = 500; duration of invasion = 100 steps; variation coefficient of species population growth rates = 0.5; local replacement proportion = 0.7.

species (see also Bell 2000). Field data do indicate that invasibility may be related to evenness, although both positive (Robinson *et al.* 1995) and negative (Smith *et al.* 2004) relationships have been reported. The null model presented confirms that skew of the abundance distribution and different invasibilities can be because of the same underlying process (species sorting) and a relationship between them is likely, in particular if invasibility is measured by number of individuals (Fig. 5).

Fully neutral models generally predict scale-dependent relationship between number of native and number of alien species (Fridley *et al.* 2004; Herben *et al.* 2004). The simulations here show that a completely different picture

emerges if variation in population growth rates is included and species pool is examined instead of species richness. In contrast to species richness, species pool is a manipulated (i.e. independent) variable in the model, and can therefore be used to establish a cause-and-effect relationship between the number of species in the species pool and invasibility: smaller species pools lead to communities that are more invasible, and the relationship is not scale-dependent.

The model also makes predictions about the relationship between numbers of native and exotic species. The predicted relationship is negative for any specific parameter combination (because of neutral effects of limited community size, Herben *et al.* 2004); however, it becomes positive if simulations with several values of one parameter are combined, even if community size does not change. This is because of the following mechanism. In the model, a larger native species pool leads to lower native species richness and higher dominance concentration as communities sampled from larger species pools are likely to contain faster growing species (i.e. 'stronger competitors' in the model; Fig. 5). This produces a negative relationship between native species pool size and native species richness. At the same time, these faster growing species are more likely to prevent invasions of random invaders, thus leading to a negative relationship between native species pool size and alien species richness; the result is a positive relationship between native and alien local species richness (Fig. 4). This may be seen as an example where differences in species richness of both native and alien species are because of a common mechanism that produces a positive correlation between the two. In this case, the mechanism is sampling from native species pools of different sizes, which produces communities with different proportions of strong competitors. It is unlikely that such a mechanism would directly act in the field, as positive relationships between species pool size and species richness are generally found (Zobel 1997). On the other hand, the role of the sampling process and species pool size is independent of the actual mechanism of diversity maintenance (Moore *et al.* 2001) and may lead to differences in invasion resistance under other diversity-maintenance mechanisms as well. For example, in niche based mechanisms of coexistence, if the species pool is smaller, there is also a smaller probability of containing the native species that occupies the same niche as the invader.

The distinction between local species richness and species pool should be taken into consideration whenever large differences in species pools across habitats are likely to occur. This is typically the case for oceanic island/continent or isolated/non-isolated island contrasts, but is also likely to be relevant to many contrasts within the mainland as well (see e.g. Ewald 2003). The size of species pools may also be an important difference between oceanic and terrestrial (habitat) islands; as migration is generally

much easier between habitat islands, their species pools are likely to be larger. This would explain why terrestrial islands of any habitat type, in contrast to true oceanic islands, are much less affected by invasions of alien species (Lonsdale 1999). In the present model, the native species pool of an island is treated as a fixed number. Over longer time scales, the species pool of an island is a dynamic entity and depends on long-term immigration patterns as well (MacArthur & Wilson 1967). Species pool differences may be thought of as reflecting the long-term immigration rate to the island and may be safely assumed to be slow enough to be able to be represented by a static variable (native species pool), given the massive propagule input in the past few centuries because of human activity (see e.g. Gaston *et al.* 2003).

The model shows that if a smaller pool of native species is the only difference between islands and continents, sampling effect will suffice to explain the higher invasibility of island biotas. If such a null model with no idiosyncratic differences between species (except growth rates) is able to explain differences in invasibility, it might serve as a baseline with which further analyses could be compared.

ACKNOWLEDGEMENTS

This paper greatly benefited from discussions with and/or comments from Kateřina Bímová, Rampa Etienne, Emily Farrer, Deborah Goldberg, Bohumil Mandák, Zuzana Münzbergová, Valerio De Patta Pillar, Petr Pyšek, Marcel Rejmánek, David Storch and two anonymous referees. I thank all of them. The research was supported by the GA ČR grant no 206/04/0081.

REFERENCES

- Aarssen, L.W., Laird, R.A. & Pither, J. (2003). Is the productivity of vegetation plots higher or lower when there are more species? Variable predictions from interaction of the 'sampling effect' and 'competitive dominance effect' on the habitat templet. *Oikos*, 102, 427–432.
- Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.*, 155, 606–617.
- Case, T.J. (1990). Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl. Acad. Sci. USA*, 87, 9610–9614.
- Case, T.J. (1996). Global patterns in establishment of exotic birds. *Biol. Cons.*, 78, 69–96.
- Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.
- Courchamp, F., Chapuis, J.L. & Pascal, M. (2003). Mammal invaders on islands: impact, control and control impact. *Biol. Rev.*, 78, 347–383.
- Davis, M.A., Grime, J.P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.
- Denslow, J.S. (2003). Weeds in paradise: thoughts on the invasibility of tropical islands. *Ann. Missouri Bot. Garden*, 90, 119–127.
- Ewald, J. (2003). The calcareous riddle: Why are there so many calciphilous species in the central European flora? *Folia Geobot.*, 38, 357–366.
- Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. U.S.A.*, 100, 8916–8920.
- Fridley, J.D., Brown, R.L. & Bruno, J.F. (2004). Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, 85, 3215–3222.
- Gaston, K.J., Jones, A.G., Hanel, C. & Chown, S.L. (2003). Rates of species introduction to a remote oceanic island. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 270, 1091–1098.
- Grace, J.B. (2001). Difficulties with estimating and interpreting species pools and the implications for understanding patterns of diversity. *Folia Geobot.*, 36, 71–83.
- Hector, A., Bazeley-White, E., Loreau, M., Otway, S. & Schmid, B. (2002). Overyielding in grassland communities: testing the sampling effect hypothesis with replicated biodiversity experiments. *Ecol. Lett.*, 5, 502–511.
- Herben, T., Mandák, B., Bímová, K. & Münzbergová, Z. (2004). Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology*, 85, 3223–3233.
- Hubbell, S.P. (1979). Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, 203, 1299–1309.
- Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 108, 449–460.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638.
- Law, R. & Morton, R.D. (1996). Permanence and the assembly of ecological communities. *Ecology*, 77, 762–775.
- Lepš, J., Brown, V.K., Len, T.A.D., Gormsen, D., Hedlund, K., Kailová, J. *et al.* (2001). Separating the chance effect from other diversity effects in the functioning of plant communities. *Oikos*, 92, 123–134.
- Levine, J.M. & D'Antonio, C.M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.
- Levine, J.M., Kennedy, T. & Naeem, S. (2002). Neighborhood scale effects of species diversity on biological invasions and their relationship to community patterns. In: *Biodiversity and Ecosystem Functioning – Synthesis and Perspectives* (eds Loreau, M., Naeem, S. & Inchausti, P.). Oxford University Press, Oxford, UK. pp. 79–91.
- Lonsdale, W.M. (1999). Global patterns of invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.
- MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, PA.
- McCullagh, P. & Nelder, J.A. (1989). *Generalized Linear Models*. Chapman & Hall, New York.
- Moore, J.L., Mouquet, N., Lawton, J.H. & Loreau, M. (2001). Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos*, 94, 303–314.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000). Plant diversity increases resistance to invasion in the absence of covarying factors. *Oikos*, 91, 97–108.
- Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996). The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, 75, 111–117.

- Polley, H.W., Wilsey, B.J. & Derner, J.D. (2003). Do species evenness and plant density influence the magnitude of selection and complementarity effects in annual plant species mixtures? *Ecol. Lett.*, 6, 248–256.
- Robinson, G.R., Quinn, J.F. & Stanton, M.L. (1995). Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology*, 76, 786–794.
- Rosenzweig, M. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- Sale, P.F. (1977). Maintenance of high diversity in coral reef fish communities. *Am. Nat.*, 111, 337–359.
- Sax, D.F. (2001). Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *J. Biogeogr.*, 28, 139–150.
- Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.
- Smith, M.D. & Knapp, A.K. (2001). Size of the local species pool determines invasibility of a C-4-dominated grassland. *Oikos*, 92, 55–61.
- Smith, M.D., Wilcox, J.C., Kelly, T. & Knapp, A.K. (2004). Dominance not richness determines invasibility of tallgrass prairie. *Oikos*, 106, 253–262.
- Sol, D. (2000). Are islands more susceptible to be invaded than continents? Birds say no. *Ecography*, 23, 687–692.
- Tilman, D., Lehman, C.L., Thompson, K.T. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. U.S.A.*, 94, 1857–1861.
- Wilson, J.B. & Anderson, B.J. (2001). Species-pool relations: like a wooden light bulb? *Folia Geobot.*, 36, 35–44.
- Zobel, M. (1997). The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.*, 12, 266–269.

Editor, Thomas Miller

Manuscript received 14 March 2005

First decision 7 April 2005

Manuscript accepted 28 April 2005