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BIODIVERSITY RESEARCH

Past and future of predictions in plant invasions: a field test by time

PETR PYŠEK *Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Pruhonice, Czech Republic. E-mail: pysek@ibot.cas.cz*

Abstract. Intensive interest in the alien flora of the Czech Republic stimulated one of the earliest attempts (in the early 1970s) to predict potential invaders of arable land. Another paper published recently by the same research team using the same methodology provides a relatively unique possibility to assess the success of these predictions after a quarter of a century. The predictions were successful for 39.3% of the 28 species included, while 60.7% of invasion cases must be considered as failures. Prediction was rather unsuccessful for the members of *Asteraceae* (14.3%), and more correct for annuals/biennials (45.5%) than for perennials (16.7%). No pattern was found with respect to the area of origin. The results indicate that past predictions based largely on intuition were less successful than modern prediction systems using the knowledge of a large number of characters and carried out using advanced computation methods. The correct identification of invaders using such systems reaches values between 61% and 91%.

Key words. Biological invasions, screening systems, prediction, agricultural weeds, Czech Republic, Central Europe.

INTRODUCTION

Invasion ecology, a relatively young and expanding field of ecology, deals not only with fundamental theoretical principles (Rejmánek, 1996; Richardson *et al.*, 2000), and global patterns (Pyšek, 1998; Lonsdale, 1999), but also has important practical connotations (Cronk & Fuller, 1995; Perrings *et al.*, 2000). Predictions of the future behaviour of introduced plants has long attracted the attention of ecologists (Daehler & Strong, 1993; Mack, 1996), and perspectives vary from awareness of shortcomings (Smith *et al.*, 1999; Williamson, 1999) to promising attempts at identifying potential invaders (Rejmánek & Richardson, 1996).

Early analyses, in the late 1980s, concluded that reliable *a priori* predictions are difficult to make, because there is no consistent set of characteristics shared by invasive species (Crawley, 1987). However, it has been demonstrated that to a certain extent, predictions are possible, namely, if variation in an invader's characteristics is reduced by concentrating on particular life forms and/or taxonomical groups (Roy *et al.*, 1991; Rejmánek, 1995; Rejmánek & Richardson, 1996). The 1990s yielded several promising region-based screening systems which represent starting points in the search for a general model for predicting invasive plants (Daehler & Carino, 2000).

Predictions are relatively easy to make but difficult to test. Invasion ecology is a young field and most of the *a priori* predictions were made too recently for us to know whether they were accurate or not. The present paper reports on a rather exceptional data set from the Czech Republic in central Europe which facilitates a test of invasion prediction.

The data

Floristic research focused on alien plants in the Czech Republic has yielded two data sets, representing together a unique case which makes it possible to test predictions of invasiveness after a quarter of a century. Intensive interest in alien flora and recognition of their potentially negative impacts stimulated probably the earliest serious Central European attempt to predict potentially invasive plants (Hejný *et al.*, 1973) in which further spread on arable soil might have been expected; the potential for this spread was claimed as the main criterion for a species being included on the list. This research was stimulated by a need to assess potential impact of alien species on agricultural production in the country. Such plants were officially termed 'quarantine weeds' and state authorities were supposed to take measures preventing further spread (Hejný *et al.*, 1973).

A similar volume focused on invasive alien plants was published recently (Jehlík, 1998); this contribution updates the distribution of most species included in the first volume, and adds additional species. Both works give particular localities with the year of collection for most species included. In the present paper, the latter volume was used for evaluating changes in the distribution of species presented in the former work.

This provides us with a relatively unique possibility to assess the success of the predictions made in the 1970s. The following circumstances make the data valuable from the comparative perspective.

The list of 'quarantine' species was compiled in the 1970s purely for practical reasons. Invasion biology represented a promising field in which research and its practical outputs could have been closely related, and this was an important demand on scientific research in the Czech Republic at that time. No one anticipated that the list would be subjected to any scientific testing in the future. Hence it perfectly meets the main reason the predictions are made, i.e. practical use.

Both data sets were compiled by the same group of people, or by workers belonging to the same workplace and scientific school, using the same methods. The data on distribution and abundance were taken mostly from herbarium specimens (namely in the case of taxonomically critical species) or from the authors' own research, thus avoiding errors through misidentification of species. The same sources were used for all species, making the data directly comparable.

Almost a quarter of a century separates the two studies. This is enough time to make such an assessment because in the contemporary Czech landscape, the invasion of species with good spreading potential would have been realized during the last 23 years.

The present paper summarizes the occurrence of 28 alien species in two successive periods: (i) until 1972 when the work by Hejný *et al.* (1973) was published (Period I); and (ii) 1973–95 (Period II) when the deadline for the data included in Jehlík (1998) was closed.

The number of localities was recorded for each species in both periods. If further records come from the same locality, only the earliest one was considered. Hence the localities reported for the latter period represent new sites. The assumption that once an alien species reaches a region, it is potentially able to occur there, seems justified in species that are considered potential invaders (Pyšek *et al.*, 2001). This approach makes it possible to compare both periods (i.e. before and after the prediction has been made) and express the percentage increase in the number of localities.

A species was considered to have increased when it occupied at least double the number of sites during Period II, compared to Period I. This criterion was applied strictly, but in one case it might not reflect precisely the actual distribution of a species in the country and its status (*Veronica filiformis* would be considered invasive if a detailed knowledge of species dynamics was taken into account, see, Pyšek & Prach (2001). However, a preference was made for using a consistent measure for all species.

RESULTS

Viewed from today's perspective, successful prediction means that the species was included in the original list compiled at the end of Period I, be it rare or common then, and it has markedly increased its distribution during the Period II. This group (recognized invasiveness, S) includes 11 species, of the total number of 28. The remaining 17 species must be considered as failures (not recognized noninvasiveness, F): they were included on the list but the prediction failed because they have not become noxious pests (Table 1). The rate of correct predictions, calculated as S/(S + F) was therefore 39.3%.

The species considered belong to 12 plant families, three of which were represented by at least four species. Comparison of the two groups

Table 1 Evaluation of predictions made in 1973 for alien weeds by Hejný *et al*. (1973). Number of localities reported for 28 species from the territory of the Czech Republic in 1972 (when the first book went to print) was compared with those reported as new in 1973–95 (deadline for data used in Jehlík, 1998). Prediction for particular species is evaluated: S — successful prediction: the species was in 1973 correctly identified as invasive; F — prediction failure: the species was incorrectly classified as potential invader but did not spread as expected. NA — number of localities was available in neither of the original sources but the trend (increase or not) is obvious. If the increase in the number of localities between the two periods exceeds 100% (i.e. the number of records was at least doubled during 1973–95), the species was considered as spreading. *species was not included in Jehlík *et al*., 1998 because it was no longer considered a threat. Species are arranged alphabetically within the prediction success categories

Species	Family	LF	Area of origin	Loc. no. 1972	Loc. no. 1973–95	Loc. total	% increase	Prediction
Abutilon theophrasti	Malvaceae	an	Asia	27	66	93	244	S
Amaranthus albus	Amaranthaceae	an	S North America	NA	NA	—	—	S
Amaranthus blitoides	Amaranthaceae	an	W North America	39	70	109	179	S
Amaranthus powellii	Amaranthaceae	an	W North & South America	NA	NA	—	—	S
Ambrosia artemisiifolia	Asteraceae	an	North America	55	101	156	184	S
Bidens frondosa	Brassicaceae	an	North America	NA	—	—	—	S
Bunias orientalis	Brassicaceae	bi	E, SE Europe, Siberia	NA	NA	—	—	S
Commelina communis	Commelinaceae	an	E Asia	13	84	97	646	S
Cuscuta epithymum var. trifolii	Cuscutaceae	an	Mediterranean	NA	NA	—	—	S
Setaria macrocarpa	Poaceae	an	E Asia	22	63	85	286	S
Sisymbrium volgense	Brassicaceae	per	E Europe	31	52	83	168	S
Acroptilon repens[1]	Asteraceae	per	E Europe, Asia	1	2	3	200	F
Amaranthus viridis	Amaranthaceae	an	South America	11	5	16	45	F
Ambrosia trifida	Asteraceae	an	North and Central America	16	12	28	75	F
Artemisia annua	Asteraceae	an	E Asia	75	22	97	29	F
*Artemisia sieversiana**	Asteraceae	an, bi	E Europe, Asia	32	—	—	—	F
*Dracocephalum thymiflorum**	Lamiaceae	an	E Europe, Asia	4	—	—	—	F
*Echinochloa coarctata**	Poaceae	an	Asia	1	—	—	—	F
*Chenopodium missouriense**	Chenopodiaceae	an	North America	4	—	—	—	F
Iva xanthiifolia	Asteraceae	an	North America	NA	NA	—	—	F
Lactuca tatarica	Asteraceae	per	SE Europe, Asia	8	7	15	88	F
*Lepidium densiflorum**	Brassicaceae	an, bi	North and Central America	NA	—	—	—	F
*Lepidium virginicum**	Brassicaceae	an, bi	North and Central America	44	—	—	—	F
Orobanche cumana[2]	Orobanchaceae	an	SE Europe, Mediterranean, Asia	0	0	—	—	F
*Rapistrum rugosum**	Brassicaceae	an, bi	Mediterranean, SE Europe, SW & C Asia	47	—	—	—	F
Rumex triangulivalvis	Polygonaceae	per	North America	30	18	48	60	F
Sorghum halepense	Poaceae	per	Mediterranean, Asia M, C Asia	49	36	85	73	F
Veronica filiformis	Scrophulariaceae	per	Caucasus, Asia Minor	129	87	216	67	F

[1] *Acroptilon* was not classified on the basis of the 100% increase criterion because of low number of localities; [2] *Orobanche cumana* was predicted as an invasive weed in 1972 despite being recorded from no localities in the country; an = annual, bi = biennial, per = perennial.

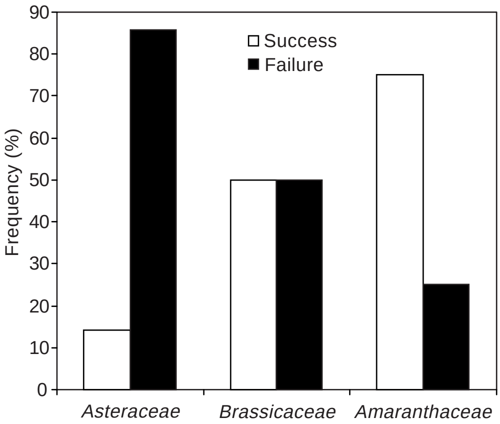

Fig. 1 Summary of prediction success/failure with respect to the taxonomical position of species. The height of the bars represents the proportion of successful and failed predictions in particular families. Only families represented by at least four species in the whole data set are displayed. See Table 1 for particular species.

(successful predictions vs. failures) from the perspective of taxonomical position shows that the prediction rate for *Asteraceae* was only 14.3% (of the seven representatives included in 1972, only one was predicted correctly). The opposite holds for *Amaranthaceae*; three of the four species from this family were classified correctly. *Brassicaceae* showed no pattern with respect to the prediction success (Fig. 1).

Some pattern was detectable with respect to life forms, although the difference was not statistically significant ($\chi^2 = 1.64$, d.f. = 1, $P = 0.20$) due to the low number of species: the ratio between successful and failed predictions in annuals was 45.5 : 54.5, while in perennials it was 16.7 : 83.3. No differences were found with respect to the area of origin: the rate of successful prediction for Eurasian species was 37.5%, while the corresponding figure for taxa from the Americas was 41.7%. On a finer geographical scale, only one of four Mediterranean species was predicted correctly.

DISCUSSION

Screening systems were recently developed independently for woody plants of South African fynbos shrublands (Tucker & Richardson, 1995) and of North America (Reichard & Hamilton, 1997) as well as for the alien flora of Australia (Pheloung *et al.*, 1999). The efficiency of these systems was tested on Hawaiian alien flora by Daehler & Carino (2000). Using the North American and Australian systems for predicting invasiveness in Hawaii yielded 82% and 91% correct classifications, respectively. The South African screening system predicted only 61% of the Hawaiian invaders (probably because it was designed for the most specific ecosystem of the three — only fire-prone shrublands within the fynbos biome). Even if we consider that the former two systems were developed for woody plants, and their predictions are therefore difficult to compare with results obtained for herbaceous weeds of arable land from another geographical region, there remains the Australian screening applicable for plant invaders regardless of life form. Comparability of results presented here is further ensured by the fact that Daehler & Carino (2000) tested the systems by using aggressive invaders in Hawaii and Hejný *et al.* (1973) compiled their lists with a goal of including potentially serious agricultural pests of alien origin. In both cases, the goal was to predict the likely behaviour of immigrant species based on any available information (Daehler & Carino, 2000). However, Pheloung *et al.* (1999) and Daehler & Carino (2000) pointed out that there are two important rates associated with prediction: (i) the rate of correctly predicting invaders as invaders and (ii) the rate of correctly identifying noninvaders as noninvaders. These two rates differ and success rates tend to be higher in identifying invaders.

Unfortunately, when working with a real data set such as the present one from the Czech Republic, these rates are difficult to identify reliably. The former figure, i.e. correctly predicting invaders, was of relevance to Hejný *et al.* (1973) for practical reasons. Assuming that their goal was to include *all* potential invaders, it would be expressed as the ratio of invaders correctly recognized in 1972 (i.e. 11 species) to the total number of potential invaders. The denominator, however, remains to be identified. Jehlík (1998) added eight species to the 1972 list, and analysis of the number of their localities revealed more than 100% increase in

Period II[1]. If we consider these as 'nonrecognized invaders', the rate of recognized invasiveness by Hejný *et al.* (1973) would be 11/19 = 57.9%. However, the realistic value is undoubtedly much lower because there are certainly more invasive species in the Czech Republic which were not recognized by the authors of the original list. Theoretically, the denominator should contain the total current number of invasive species in the Czech flora. Some estimate of this figure can be made. Pyšek & Prach (2001) recently estimated the number of invasive species in the Czech flora at 65, although they used slightly different and more sophisticated criteria than simply the increase in the number of localities (see Richardson *et al.*, 2000). Taking their list as an estimate of the total number of invaders would yield the rate of correctly predicting invaders as 11/65 = 16.9%. However, this value is somewhat underestimated because the focus in the study of Hejný *et al.* (1973) was on human-made habitats, and arable land in particular. It seems more realistic (and fair to the authors of the 1970s list) to restrict the set of invasive species given by Pyšek & Prach (2001) to those that can occur potentially in the kind of habitats considered by Hejný *et al.* (1973). By doing this, we are left with a ratio of approximately 11/43, i.e. the recognized invasiveness of about 25%.

Recognized noninvasiveness (i.e. correctly identifying noninvaders as noninvaders) is irrelevant for the present paper because no attempt to predict noninvasive species was made by Hejný *et al.* (1973). This figure, however, cannot be reliably identified for a real data set anyway because it concerns noninvaders for which good data are usually more difficult to obtain than for invaders. Theoretically, this value would be represented by the proportion of correctly identified noninvasive species (had such prediction been made) of the total number of noninvasive aliens present at the territory of the country at the time of prediction. In this case, the denominator is even more difficult to estimate but the rate of successful prediction would be very high because it can easily be assumed that of the total number of alien species in the Czech flora, currently estimated at about 1200 (Pyšek, Mandák & Sádlo, unpublished data), the vast majority never become invasive. Nevertheless, it appears that the rate of correctly identifying noninvaders as noninvaders can only be assessed for an *a priori* defined species set (such as those used in simulation models or plants legally introduced across a country border) but hardly on the data set like the present one.

The prediction rate calculated for the present data, giving the value 39.3%, hence reflects the rate of correct prediction among species on the list of Hejný *et al.* (1973). The arbitrary measure used in the present paper, i.e. 100% increase in the number of localities in a quarter of century, seems justified as it reasonably reflects the classification of invasive species at the territory considered which was based on a number of other criteria (Pyšek & Prach, 2001).

Although the prediction rates which would be directly comparable with results of Daehler & Carino (2000) can only be estimated for the present data set, the distinction in the success of both approaches is obvious. It can be theorized that in a practical situation reported here, 25–50% invaders could be correctly predicted. This value can be compared with 82% and 91% reported by Daehler & Carino (2000) rather than with 61% yielded by the programme designed specifically for fire-prone shrublands in the fynbos biome of South Africa. The marked difference in the rate of successful prediction between the recent sophisticated systems based on evaluation of the number of biological and ecological characters (life history, biogeography, habitat characteristics, invasiveness elsewhere) and using advanced computing techniques on one hand, and intuitive, field-knowledge-based *a priori* predictions on the other, clearly indicates much better applicability of the former. These systems ensure that a large number of noninvasive species which potentially can bring economic benefits would be accepted for introduction while more costly invaders could be rejected from introduction (Daehler & Carino, 2000).

The successful or failed predictions seem to be rather randomly distributed among the species included in the 1970s paper as far as their origin

[1] *Cannabis ruderalis* (17 localities in Period I, 29 localities in Period II — 171% increase), *Consolida orientalis* (34, 71–209%). *Erigeron annuus* (data not given, but increasing), *Hirschfeldia incana* (12, 20–167%), *Kochia scoparia* subsp. *densiflora* (25, 75–300%), *Orobanche minor* (24, 102–425%), *Panicum capillare* subsp. *capillare* (10, 45–450%), *Rumex patientia* (10, 34–340%).

is concerned. However, a slight taxonomical bias, namely against *Asteraceae*, should not be over-estimated because the number of representatives in particular families was rather low. Nevertheless, the results indicate that invasiveness of annual species might be easier to predict than that of perennials.

The Czech Republic is considered one of the important gateways for introducing species of eastern origin farther to the north-west of Europe (Pyšek & Prach, 2001). Introduction of alien species to the country proceeded by several distinct migration routes. North American species have been coming along the Elbe River, transported mainly with grain and soybeans. Many species, agricultural weeds in particular, came from the south-eastern Pannonian region. Finally, another distinct group of species is those of eastern origin, coming from the Far East and Asia. These were introduced with grain and other goods imported from Russia (Jehlík & Hejný, 1974). The described situation has changed at the turn of the 1990s, due to political changes in the country (1989) and the subsequent shift of trade focus from the East to the West. The relative importance of particular migration routes has changed, and this could have affected the outcome of previous predictions. However, these changes came at the very end of Period II (1972–95, as defined in the present paper), i.e. only a few years before the data collection for the survey reported in Jehlík (1998) was terminated. In addition, considering some inertia in the functioning of such large-scale dispersal phenomena, the results reported here hardly could have been affected in a serious way.

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