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BIODIVERSITY RESEARCH

Predicting invasions by woody species in a temperate zone: a test of three risk assessment schemes in the Czech Republic (Central Europe)

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ABSTRACT

To assess the validity of previously developed risk assessment schemes in the conditions of Central Europe, we tested (1) Australian weed risk assessment scheme (WRA; Pheloung *et al*. 1999); (2) WRA with additional analysis by Daehler *et al*. (2004); and (3) decision tree scheme of Reichard and Hamilton (1997) developed in North America, on a data set of 180 alien woody species commonly planted in the Czech Republic. This list included 17 invasive species, 9 naturalized but non-invasive, 31 casual aliens, and 123 species not reported to escape from cultivation. The WRA model with additional analysis provided best results, rejecting 100% of invasive species, accepting 83.8% of non-invasive, and recommending further 13.0% for additional analysis. Overall accuracy of the WRA model with additional analysis was 85.5%, higher than that of the basic WRA scheme (67.9%) and the Reichard–Hamilton model (61.6%). Only the Reichard–Hamilton scheme accepted some invaders. The probability that an accepted species will become an invader was zero for both WRA models and 3.2% for the Reichard–Hamilton model. The probability that a rejected species would have been an invader was 77.3% for both WRA models and 24.0% for the Reichard–Hamilton model. It is concluded that the WRA model, especially with additional analysis, appears to be a promising template for building a widely applicable system for screening out invasive plant introductions.

Keywords

Alien plants, biological invasions, Central Europe, forestry, invasive species, prediction, weed risk assessment.

INTRODUCTION

The search for characteristics of invasive species (Crawley *et al*., 1996; Rejmánek, 1996) is a central issue in invasion biology, as it determines our ability to predict the invasion success of alien plants in new regions (Richardson & Pyšek, 2006). Over the last 30 years, attempts to identify traits of successful invasive species shifted from studies focused on all vascular plants (Baker, 1974; Pyšek *et al*., 1995; Crawley *et al*., 1996) to those dealing with restricted taxonomic and/or life-form groups (Rejmánek & Richardson, 1996; Grotkopp *et al*., 2002; Richardson & Rejmánek, 2004; Rejmánek *et al*., 2005b), often in geographically and ecologically specified areas (Kowarik, 1995; Tucker & Richardson, 1995). Predicting which species will invade has been a long-standing goal of ecologists (Kolar & Lodge, 2001); this knowledge is translated into risk assessment schemes that attempt to predict the behaviour of alien species in secondary areas (Daehler & Carino, 2000). Only a small proportion of introduced alien species becomes naturalized and invasive (di Castri, 1989; Williamson, 1996). It has been proposed that about one of 10 introduced species becomes casual, one of 10 casuals naturalized, and one of 10 naturalized aliens becomes a pest (Tens Rule: Williamson & Fitter, 1996; Williamson, 1996). In the same vein, about 1% of introduced plants are estimated to invade natural vegetation (Kowarik, 1995). The risk assessment schemes attempt to identify this small fraction of species that can be potentially harmful to natural vegetation and invade large areas.

Two groups of risk assessment models can be recognized, based on the methods used and the phase of the invasion process they target. (1) Pre-introduction models predict the potential behaviour of a species prior to its introduction (Scott & Panetta, 1993; Pheloung, 1995; Tucker & Richardson, 1995; Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997; Pheloung *et al*., 1999; Daehler & Carino, 2000; Reichard, 2001; Daehler *et al*., 2004; Weber & Gut, 2004). Such approaches often use statistical discrimination analysis and classification and regression trees

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(CARTs). These schemes are often based on rating systems (e.g. Pheloung, 1995) or on hierarchical decision trees (e.g. Reichard & Hamilton, 1997); the only screening procedure based on biological plant attributes and some ecological interactions of woody plants is in Rejmánek & Richardson (1996; see also Richardson & Rejmánek, 2004). (2) Post-introduction models focus on predicting the future behaviour of species that have already become naturalized or invasive in the new area. Such schemes typically rely on geographical information systems (Higgins *et al*., 1999; Sax, 2001; Windrlechner, 2001; Windrlechner & Iles, 2002; Rouget & Richardson, 2003; Dark, 2004; Marais *et al*., 2004; Rouget *et al*., 2004; Windrlechner *et al*., 2004). In addition, empirical schemes based on investigators' experience have been used (Hejný *et al*., 1973), but the predictive power of such attempts was rather limited compared to sophisticated statistical and geographical approaches (Pyšek, 2001).

Rapid development of computing facilities and increasing availability of databases allowed for increasing generality of recently developed screening models (Daehler & Carino, 2000). The Weed Risk Assessment (WRA) scheme developed for Australia and New Zealand (Pheloung, 1995; Pheloung *et al*., 1999) and successfully tested in Hawaii and other Pacific islands (Daehler & Carino, 2000; Daehler *et al*., 2004) is a promising tool for assessing the risks from plant invasions. This study explores predictive potential of WRA in a biogeographical zone that has not been subject to testing so far and compares it with other schemes. We used alien woody species commonly planted in the Czech Republic, Central Europe, a country prone to invasions by alien species (Pyšek *et al*., 2002; Mandák *et al*., 2004; Chytrý *et al*., 2005). Invasions by woody species often alter the functioning of invaded ecosystems (Williamson, 1999; Richardson *et al*., 2000). On the other hand, there is a strong requirement for finding non-harmful woody species for commercial use (Richardson, 1998; Richardson *et al*., 2004a). These two contradicting aspects make the need for reliable weed risk assessment schemes for woody plants particularly urgent. Moreover, woody plants are a frequently used test group (Rejmánek & Richardson, 1996; Reichard & Hamilton, 1997; Reichard, 2001; Windrlechner, 2001; Windrlechner & Iles, 2002; Windrlechner *et al*., 2004; Rejmánek *et al*., 2005a) because of detailed records of introduction history and plentiful data on biology, ecology, and adaptation to climate of target areas (Richardson *et al*., 2004b). This study aims at exploring the extent to which risk assessment schemes developed in other parts of the world and for different ecological and climatic conditions are useful under the temperate conditions of Central Europe.

METHODS

Risk assessment schemes tested

Three models were chosen for testing: (1) weed risk assessment scheme (WRA) (Pheloung, 1995; Pheloung *et al*., 1999); (2) WRA with additional decision tree analysis of species recommended for further evaluation (Daehler *et al*., 2004; fact sheets available at http://www.botany.hawaii.edu/faculty/daehler/WRA); and (3) Reichard and Hamilton's decision tree (Reichard & Hamilton, 1997; Reichard, 2001). The former two models were selected because they have already been tested in a number of regions around the world (Pheloung *et al*., 1999; Daehler & Carino, 2000; Daehler *et al*., 2004). Proving them successful under temperate conditions of Central Europe would be a further step to their wider applicability. Reichard and Hamilton's scheme was used because it was primarily designed for woody species in the temperate zone (i.e. for conditions applicable to our study region).

(1) The WRA model (Pheloung *et al*., 1999) was developed for Australian and New Zealand alien plants. It consists of 49 questions divided into sections on biogeography, biology/ecology, and traits potentially contributing to the invasiveness. Answers are scored from −3 to +5 and the species is accepted for introduction (score < 1), rejected (> 6), or recommended for further analysis (1–6). A minimum of 10 answers are needed for a species to be evaluated: at least two in the biogeography section, two in traits section and six in biology/ecology. However, for proper evaluation it is recommended that at least one-third of questions are answered.

(2) WRA with additional decision tree analysis (further referred to as 'WRA+Daehler') resulted from testing the WRA in Hawaii (Daehler & Carino, 2000) and other Pacific islands (Daehler *et al*., 2004). Species qualified by the WRA for further analysis are subjected to an additional questionnaire, built as a binary decision tree and resulting in the same classification as the WRA scheme, i.e. accept, reject or recommended for further analysis.

(3) Reichard and Hamilton's decision tree was built for woody species in North America (Reichard & Hamilton, 1997) and Hawaii (Reichard, 2001). It consists of seven questions in a binary (yes/no) tree. Similarly to the WRA analysis, a species is recommended for acceptation, rejection, or further analysis and monitoring.

In our study, questions related to geography and climate were modified to reflect the conditions of the target area. In WRA, suitability of species to Australian climate was changed to suitability to Central European climate (question 2.01) and origin or naturalization in regions with extended dry periods was changed to origin or naturalization in regions with temperate climate (question 2.04). In the Czech Republic, the mean annual temperature is 7.3 °C (min. 0.4 °C, max. 10.1 °C), and the mean annual precipitation is 672.6 mm (min. 384.6, max. 1497.8) (Czech Hydrometeorological Institute, http://www.chmu.cz). The presence of effective natural enemies in Australia was changed to the presence of effective natural enemies in the Central Europe (question 8.05). In the Reichard–Hamilton scheme, North America was changed to Central Europe in questions related to invasiveness of the species outside the target region and to its membership in a genus or family with another strongly invasive representative. The question about origin in parts of North America other than the region of the proposed introduction was changed to origin of the species in other parts of Europe.

Following present trends in taxonomy and nomenclature, a taxonomic concept of broader genera was adopted, i.e. *Prunus* s.l. (including *Cerasus, Padus,* and *Laurocerasus*), *Acer* (*Acer*, *Negundo*), and *Cornus* (*Cornus*, *Swida*). This approach allows for better reflection of evolutionary relationships than concept of narrow genera, when evaluating invasiveness of closely related taxa. Status of hybrids followed the approach of Pyšek *et al.* (2004), i.e. they were considered native to Europe only if both parent species originated from this continent.

Species tested

The data set comprised 180 alien woody species frequently planted and acclimatized in the Czech Republic: all 28 species that are at present widely planted for timber in forests (Křivánek *et al.*, 2006), and 152 species commonly planted in parks and gardens. The latter group was selected from the total of 1691 park and garden woody species on the basis of their residence time, frequency of planting, and horticultural importance. Only species planted in the Czech Republic for at least 60 years and well adapted to the conditions of target region were considered (a similar time criterion as applied by Reichard & Hamilton, 1997). Species only planted in specialized collections, not offered in garden catalogues, or planted in parks in the Czech Republic were excluded. The selection was based on summarizing literature sources (Koblížek, 2000), on 121 garden catalogues, covering the period since year 1852 up to present, and on the occurrence of woody species in 823 chateau parks in the countryside (Hieke, 1984, 1985) and in 13 large parks of Prague (B. Gregorová *et al.*, unpublished). An effort was made to include species with comparable intensity of planting in the country, implying comparable propagule pressure. Under such assumption, the potential invasiveness of species does not depend on the frequency of planting but on their geographical and ecological traits.

Concerning the invasion status, 17 species on the list were invasive, 9 naturalized but non-invasive, 31 casual aliens, and 123 were never reported to escape from cultivation (see Appendix S1 in Supplementary Material; status taken from Pyšek *et al.*, 2002). Classification of the invasion status follows Richardson *et al.* (2000) and Pyšek *et al.* (2004). Casual species do not form self-replacing populations outside cultivation and rely on repeated introductions for their persistence. Naturalized species reproduce consistently and sustain populations over many life cycles without direct intervention by humans. Invasive species are a subset of naturalized, that have the potential to spread over a considerable area. Environmental weeds (pests) are alien species that invade natural vegetation, usually adversely affecting native biodiversity and/or ecosystem functioning (Pyšek *et al.*, 2004).

Taxonomic nomenclature follows Koblížek (2000).

Accuracy and reliability of tested schemes

For each scheme, accuracy and reliability for Central Europe were calculated following Smith *et al.* (1999). Accuracy indicates the probability of correct classification, i.e. the proportion of known invasive species that would be correctly assessed as invasive [$A_i = (I_r/I_t) \times 100$; where I_r is the number of invaders that were rejected by the system, and I_t was the total number of invaders assessed], and that of known non-invasive species that would be correctly identified as non-invasive [$A_n = (N_a/N_t) \times 100$; where N_a was the number of non-invader species accepted and N_t the total number of non-invaders assessed]. Overall accuracy [$A_o = (N_a + I_r)/(N_t + I_t)$], including both components, was used to compare the suitability of the schemes tested.

To set up the bottom level for the acceptance of each scheme for Central Europe, we followed overall accuracy A_o in the prime region of its development as calculated by Smith *et al.* (1999). These values were 76% for Reichard–Hamilton and 85% for the WRA scheme based on the figures from Australia and New Zealand; the latter was taken as the acceptable level of overall accuracy for our data.

Reliability takes into account that any sample of species rejected by a screening system will include a proportion of non-invasive species wrongly classified as invaders. It has two components: the probability that an accepted species will become invader, $P_{ai} = I_a/(N_a + I_a)$, and the probability that a rejected species would have been an invader, $P_{ri} = I_r/(N_r + I_r)$. When assessing the reliability of prediction schemes, the base-rate effect must be taken into account. This effect refers to the fact that it is much harder to predict rare events. The overall base-rate probability for a species to become invasive is a product of three probabilities, i.e. the rate at which it escapes from cultivation and becomes casual, the rate of naturalization, and the rate of the naturalized species becoming a pest (Smith *et al.*, 1999). The base-rate for alien woody plants in the Czech Republic was calculated following Smith *et al.* (1999) with the only difference of using the category invasive instead of pest for the latter probability. Nonetheless, as 11 of the 17 invasive species in the data set are environmental weeds with serious impact (Křivánek *et al.*, 2004), the figure obtained can be compared with those given in Smith *et al.* (1999).

RESULTS

The WRA+Daehler model provided the best results. The basic WRA model rejected all invasive species but also 3.5% (5 species) of non-invasive taxa. Sixty-four percent (91 species) of non-invaders were accepted and 32.5% (46) were suggested for further analysis. Using the WRA+Daehler model led to the final acceptance of 83.8% (119) of non-invaders; further evaluation was still needed for 13.0% (18) of species (Fig. 1, see Appendix S1 in Supplementary Material). On average, the data allowed to answer 37 questions of 49 posed by the scheme.

The Reichard and Hamilton's decision tree model was least successful. It rejected only 35.0% (6) of invasive species and 47.0% (8) were suggested for further evaluation. This model was the only one that accepted some invaders (3 species, 18.0%). One of the accepted species (*Quercus rubra*) is considered a pest in the Czech Republic (Křivánek *et al.*, 2004). The Reichard–Hamilton model accepted 65.0% (92) of non-invasive species and recommended 22.0% (31) for further evaluation. The number of non-invasive species rejected (19, i.e. 13.0%) was also highest of the three models tested (Table 1, Fig. 1).

Overall accuracy was highest for the WRA+Daehler model (85.5%); the additional analysis of species recommended for

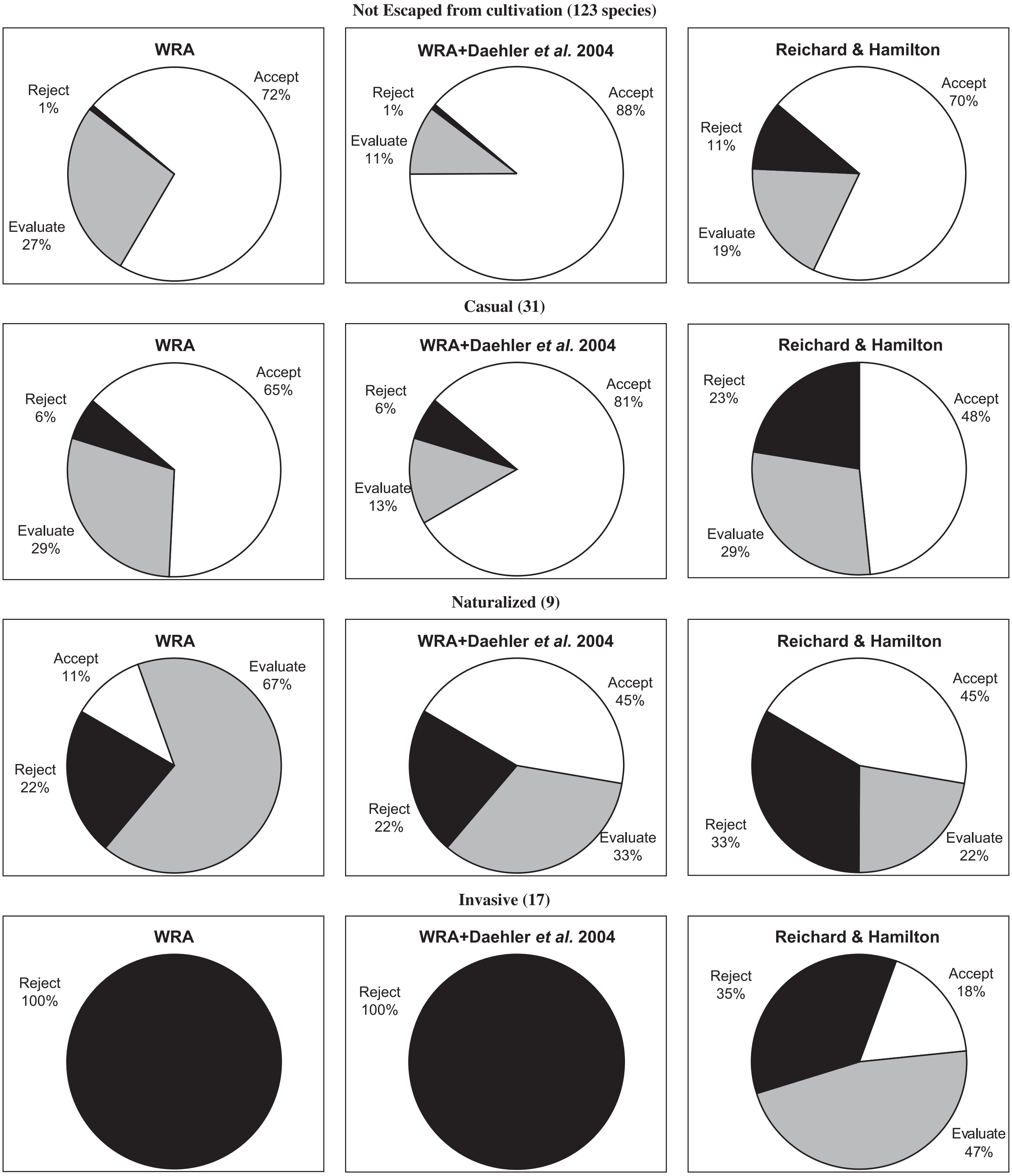

Figure 1 Results of three risk assessment schemes (see text for details) applied to 180 alien woody species commonly planted in the Czech Republic. Percentage of species rejected, accepted, or suggested for further evaluation is indicated for particular groups differing in invasion status. Definition of categories follows Richardson *et al*. (2000) and Pyšek *et al*. (2004).

further evaluation increased the accuracy of the basic WRA scheme by 17.6%. The accuracy of the basic WRA scheme (67.9%) was still higher than that of the Reichard–Hamilton model (61.6%) (Table 1).

Both WRA-based schemes rejected all invasive species, so the probability that an accepted species would become an invader was null. On the other hand, the probability that a rejected species would have been an invader was 77.3%. A low number of

Table 1 Accuracy and reliability of tested models evaluated according to Smith *et al*. (1999)

	Species number						Accuracy (%)			Reliability (%)	
Model	I_r	I_a	I_t	N_a	N_r	N_t	A_i	A_n	A_o	P_{ai}	P_{ri}
WRA	17	0	17	91	5	142	100.0	64.1	67.9	0.0	77.3
WRA+Daehler	17	0	17	119	5	142	100.0	83.8	85.5	0.0	77.3
Reichard & Hamilton	6	3	17	92	19	142	35.3	64.8	61.6	3.2	24.0

I, number of invasive species; *N*, number of non-invasive species; r, rejected; a, accepted; t, total; A_i, accuracy of correctly identifying invaders; A_n, accuracy of correctly identifying non-invaders; A_o, overall accuracy; P_{ai}, the probability that a species accepted will become an invader; P_{ri}, the probability that a rejected species would have been an invader. See text for details on particular screening models.

rejected invasive species in the Reichard–Hamilton's model yielded a 3.2% probability that an accepted species would invade but that only 24.0% of rejected species would invade (Table 1).

Of casual aliens, 6% (WRA and WRA+Daehler) and 23% (Reichard–Hamilton) were rejected. The number of casual species recommended for further evaluation was reduced from 29% (WRA) to 13% (WRA+Daehler), and 65% and 81% of casuals were accepted by WRA and WRA+Daehler, respectively. Reichard–Hamilton's model accepted 48% of casuals and 29% were recommended for further analysis. Both WRA schemes rejected 22% of naturalized species. Percentage of naturalized species recommended for acceptance by the WRA scheme (11%) increased to 45% in the WRA+Daehler model, as the number of species recommended for further evaluation decreased from 67% to 23%. Reichard–Hamilton's scheme rejected 33% of naturalized species, 45% were accepted, and 22% required further evaluation (Fig. 1).

DISCUSSION

For the reasons outlined above, our study focused on risk assessment schemes applicable to woody plants in Central Europe. Nevertheless, there are other screening systems and some of them yielded promising results: the model developed for South African fynbos vegetation (Tucker & Richardson, 1995), EPPO Pest Risk Assessment (http://www.eppo.org/QUARANTINE/quarantine.htm), or risk assessment of new environmental weeds in Central Europe (Weber & Gut, 2004). The fynbos model was designed for application to very specific conditions — fire-prone, nutrient-poor shrublands — that do not occur in Central Europe. The EPPO screening procedure was primarily developed for plant and insect pests of agricultural habitats and cannot be used to predict invasions to natural vegetation. The risk assessment scheme developed for environmental weeds in Switzerland was not used here because it is very similar to the WRA scheme and its overall accuracy, calculated for 47 plants invasive in temperate Europe and 193 aliens that have failed to naturalize in Switzerland, was as low as 65% (Weber & Gut, 2004). The present study therefore focused on testing the two models developed for Australian vegetation (Pheloung, 1995; Pheloung *et al*., 1999) and alien woody species in North America and Hawaii (Reichard & Hamilton, 1997; Reichard, 2001).

Reichard and Hamilton's decision tree is relatively easy to use. Only seven questions need to be answered, using the binary mode. In North America, 90% of 235 tested woody species were correctly assessed with this scheme, 97.1% of invasive species were rejected, and 70.8% of non-invasive were accepted; the overall accuracy was 76% (Reichard & Hamilton, 1997; Smith *et al*., 1999; but see Rejmánek *et al*., 2005a; pp. 110–111 for some problems with the categorization of species as 'non-invasive' in this scheme). The scheme is now being used in botanical gardens and horticultural practice in the USA (S. Reichard, pers. comm.). However, when applied to Central Europe, this scheme rejected only 35% of invasive species and accepted 65% of non-invasive. The overall accuracy was 14% lower than in the region for which it was developed. Primary reason for this failure could be that the model ignores climatic factors in native distribution area of tested species. Many species rejected as potentially invasive in our test of this model are not suited to the Central European climate because of severe winter seasons and frost. This, in combination with a strong emphasis on whether or not a species is invasive elsewhere, leads to misclassification of some non-invasive species as pests (see Appendix S1 in Supplementary Material). For example, *Buddleja davidii* is a serious invader in Australia, Mediterranean basin, and European regions with oceanic climate (Weber, 2003). In the Czech Republic, however, it was only reported as casual for the first time recently (Pyšek *et al*., 2002) because it is limited by frost. Other incorrectly classified harmful species are *Paulownia tomentosa* (invasive in North America; planted in the Czech Republic since 1844), *Gleditschia triacanthos* (South Africa and Australia, 1785), *Morus alba* (South Africa, 1835), and *Wisteria sinensis* (North America, 1913). All these species have been planted in the Czech Republic for a sufficiently long period to have become adapted to the local climate.

In our data set, the criterion of being invasive elsewhere appeared less important than suggested in the Reichard–Hamilton scheme; this criterion is also included in the WRA screening procedure. In our tested group, 38 species are reported as invasive elsewhere (Reichard, 1997; Bingelli *et al*., 1998; Haysom & Murphy, 2003; Weber, 2003). All seven species reported as invasive both elsewhere and in the Czech Republic were rejected by both WRA schemes, and six of them by the Reichard–Hamilton scheme, too. On the other hand, the Reichard–Hamilton scheme rejected also 13 of 17 species not escaped from cultivation in the

Czech Republic. WRA rejected 11 not escaped species and the WRA+Daehler provided best results, rejecting only one such species. The invasive-elsewhere criterion is generally considered very important for the assessment of potentially invasive species and sometimes it is even taken as the only permanent predictor of invasion (Williamson, 1999).

Taxonomic classification is another source of bias when transferring screening system of Reichard and Hamilton from one area to another. Stressing the invasiveness of other species within the genus/family and using it as an important decision attribute make the results rather sensitive to the differences in generic concept used in different areas. Although many invasive species belong to genera containing a single invasive species, membership to a large genus becomes a sort of 'the mark of Cain' for all its representatives. The probability that a large genus includes an invasive species is higher than for small genera and the simple system of answering yes or no does not take into account how large a proportion of species within the genus are invasive. Because of the invasion of *Acer negundo* (*Negundo aceroides*) in the Czech Republic, decision on other casually occurring or even non-escaping maples was postponed to further analysis (see Appendix S1 in Supplementary Material). A pest species *Quercus rubra* is an example of the one most seriously misclassified; it was accepted while two other non-escaping oaks were recommended for further screening. The results within genera *Prunus* and *Robinia* were also biased by the 'genus invasiveness' concept. Finally, absence of vegetative growth is an attribute of non-invasiveness in the North American system. Although vegetative growth is considered as an important attribute of successful invader (Kolar & Lodge, 2001; Weber & Gut, 2004), some successful invaders in Central Europe do not reproduce vegetatively. From the tested list, this holds for *Mahonia aquifolium, Lycium halimifolium, Pinus strobus*, and *Quercus rubra*, but only the first species was rejected (see Appendix S1 in Supplementary Material). To conclude, it appears that the low number of questions on which the Reichard and Hamilton's system is based makes the scheme easy to use in situations for which it was developed, but limits its applicability elsewhere.

WRA was developed for Australia and New Zealand (Pheloung, 1995; Pheloung *et al*., 1999) and successfully tested in Hawaii and other Pacific islands (Daehler & Carino, 2000; Daehler *et al*., 2004). Pheloung *et al*. (1999) tested 370 plant species alien to Australia, representing both weeds and useful taxa from agriculture, the environment, and other sectors. All serious pests and 84% non-harmful but invasive species were rejected and only 7% of non-invasive species were rejected or recommended for further analysis. When applied to Hawaii, WRA rejected 99% of invasive species (Daehler & Carino, 2000). In other Pacific islands, 95% of invasive species were rejected and 85% of non-invasive species were accepted. By using additional decision tree, Daehler *et al*. (2004) were able to cut down the portion of species recommended for further analysis from 24% to 8%. The results yielded by the WRA model with additional decision tree in the Czech Republic were even better than in Australia and Pacific region. All invasive species were rejected and 83.8% of non-invasive were accepted. This implies that the WRA screening procedure, as modified by Daehler *et al*. (2004), might be potentially suitable for a wider range of geographical regions.

Of the 127 woody species reported as escaping from cultivation in the Czech Republic, 54 are naturalized (42.5%) and there are 11 (20.3%) pests among the latter. These values are much higher than predicted by the Tens Rule (Williamson, 1996) and compare to those found in vertebrates (Jeschke & Strayer, 2005). It implies that woody plants are very successful as invaders, compared to other plant groups. All three schemes reflected a clear trend of increasing proportion of rejected species as naturalization process progressed from casual to naturalized to invasive stage. In general, results obtained for casual and naturalized but non-invasive species are not too encouraging regardless of the scheme used. Not surprisingly, it is more difficult to predict the behaviour of species that escaped from cultivation but are not yet invasive. Many woody species have long lag-phases to invasions and the number of invasive aliens will increase in the future even if introductions ceased instantly (Kowarik, 1995). In our study, we attempted to reduce this bias by testing only those species that are planted for sufficiently long period in the Czech Republic, but it is clear that species yet to become invasive increase the variation in possible outcome of invasion, hence affecting the accuracy of the risk assessment schemes.

The overall accuracy of the best fit model (WRA+Daehler) achieved in conditions of Central Europe was 86% (compared to 68% for WRA and 62% for Reichard–Hamilton). Nevertheless, the predictive power of risk assessment schemes is higher for identifying invasive and harmful species than for finding safe non-invasive species. The level of misclassifications tends to be higher for species that will probably never become invasive than for harmful invaders; the number of potentially rejected non-invasive aliens is relatively high because of low base-rate effect of occurrence of invasive species (Smith *et al*., 1999). Data are available for the Czech Republic that allow to quantify successful transition from one step of invasion process to the next and demonstrate that predicting invasions is indeed about predicting rare events. The potential pool of woody aliens introduced to the Czech Republic includes 4360 taxa (M. Křivánek, unpublished data). Of these, only 2.9% are known to have escaped from cultivation, 1.7% persist as casuals, and 0.8% are naturalized. Only 0.4% (one in 257 species) are invasive and 0.25% (one in 396) are harmful pests. These numbers can be related to the accuracy of the three tested schemes. Of the total source pool of 4360 taxa, 4343 are currently not invasive. If the percentage of false predictions obtained by the tested schemes (Fig. 1) is approximated to these 4343 species, 608 (WRA+Daehler), 1390 (WRA), and 1650 (Reichard–Hamilton) species that are probably safe in terms of potential invasion would be rejected.

Smith *et al*. (1999) also document that a scheme can be ignored if the economic loss caused by introduction of a harmful species is not eight times higher than a loss caused by its rejection. This approach, however, does not take the identity of species in question and habitat invaded into account. The damage to natural ecosystems is in most cases irreversible, hence difficult to compare to an economic loss resulting from unrealized opportunity. The rejection of a potentially harmless species can be in many cases compensated by an introduction of another harmless species, alien or native. It is possible that continuing commercial use of some harmful species reflects the inertia of forestry authorities rather than economic reasons. For example, *Pinus strobus* has been planted in the Czech Republic for more than two centuries; it invades unique natural sandstone habitats. The invasion of this species has been one of the most dramatic by woody species in this country (Hadincová *et al*., 1997). It does not produce a good quality timber and could be replaced in many cases by aliens that are not invasive in the Czech Republic, such as *Pseudotsuga menziesii* or *Abies grandis* (Forest Management Institute 1994); yet new plantations of *P. strobus* are being established (Czech Statistical Office, 2002). This example indicates that a decision whether to introduce a prediction scheme or to discard it cannot be based solely on the value of accuracy and reliability it provides. Schemes achieving high levels of accuracy in different geographical and ecological situations, such as the WRA model elaborated by Daehler *et al*. (2004), represent a valuable tool with a capacity to diminish the risk of invasion by newly introduced species.

Our study was performed on woody species commonly planted in the Czech Republic but all the species tested are planted in a wider area of Central Europe; most of them were introduced to other parts of Europe prior to their introduction to the Czech Republic (Svoboda, 1976, 1981). This makes the results of the present study applicable to the temperate climate of Central Europe in general.

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REFERENCES

Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.

Bingelli, P., Hall, J.B. & Healey, J.R. (1998) An overview of invasive woody plants in the tropics. *School of Agricultural and Forest Sciences Publication* **13**. University of Wales, Bangor, 83 p.

di Castri, F. (1989) History of biological invasions with special emphasis on the Old World. *Biological Invasions: a global perspective* (ed. by J.A. Drake *et al.*), pp. 1–30. John Wiley and Sons, Chichester.

Chytrý, M., Pyšek, P., Tichý, L., Knollová, I. & Danihelka, J. (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia*, **77**, 339–354.

Crawley, M.J., Harvey, P.H. & Purvis, A. (1996) Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **351**, 1251–1259.

Czech Statistical Office (2002) *Forestry in the Czech Republic: statistical review for year 2002*. [URL: http://www.czso.cz/] (Last accessed April 2004).

Daehler, C.C. & Carino, D.A. (2000) Predicting invasive plants: prospects for general screening system based on current regional models. *Biological Invasions*, **2**, 93–102.

Daehler, C.C., Denslow, J.S., Ansari, S. & Kuo, H.-C. (2004) A risk assessment system for screening out invasive pest plants from Hawai'i and other Pacific Islands. *Conservation Biology*, **18**, 360–368.

Dark, S.J. (2004) The biogeography of invasive alien plants in California: an application of GIS and spatial regression analysis. *Diversity and Distributions*, **10**, 1–9.

Forest Management Institute (1994) *Possible use of introduced alien woody species in forestry in the Czech Republic*. Ústav pro hospodáøskou úpravu lesù — Forest Management Institute, Brandýs nad Labem (In Czech).

Grotkopp, E., Rejmánek, M. & Rost, T.L. (2002) Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (Pinus) species. *The American Naturalist*, **159**, 396–419.

Hadincová, V., Dobrý, J., Halzélyová, D., Härtel, H., Herben, T., Krahulec, F., Kyncl, J., Moravcová, L., Šmilauer, P. & Šmilauerová, M. (1997) Invasive species *Pinus strobus* in protected area Labské Pískovce. *Invasive alien plants in the Czech flora*. (ed. by P. Pyšek and K. Prach), pp. 63–79. Zprávy České Botanické Společnosti Praha 32, Materiály 14 (In Czech).

Haysom, K.A. & Murphy, S.T. (2003) The status of invasiveness of forest tree species outside their natural habitat: a global review and discussion paper. *Forest Health and Biosecurity Working Paper FBS/3E*, 1–80. Forestry Department, FAO, Rome.

Hejný, S., Jehlík, V., Kopecký, K., Kropáč, Z. & Lhotská, M. (1973) Quarantine weeds of the Czechoslovakia. *A Study of the Czech Academy of Sciences*, **1973/8**, 1–156 (In Czech).

Hieke, K. (1984) *Czech chateau parks and their woody species*. SZN Praha, Praha (In Czech).

Hieke, K. (1985) *Moravian chateau parks and their woody species*. SZN Praha, Praha (In Czech).

Higgins, S.I., Richardson, D.M., Cowling, R.M. & Trinder-Smith, T. (1999) Predicting the landscape-scale distribution of alien plants and their threat to plant diversity. *Conservation Biology*, **13**, 303–313.

Jeschke, J.M. & Strayer, D.L. (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences USA*, **102** (20), 7198–7202.

Koblížek, J. (2000) *Conifers and hardwoods in our gardens and parks*. Freedom DTP Studio and SURSUM, Tišnov (In Czech).

Křivánek, M., Pyšek, P. & Jarošík, V. (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. *Conservation Biology*, (in press).

Křivánek, M., Sádlo, J. & Bímová, K. (2004) Control of invasive plant species. *Management of Natura 2000 habitats* (ed. by A. Háková), pp. 23–27,127–131. Planeta, **XII/8,** MŽP ČR Praha (In Czech).

Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, **16**, 199–204.

Kowarik, I. (1995) Time lags in biological invasions with regard to the success and failure of alien species. *Plant invasions: general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 15–38. SPB Academic Publishing, Amsterdam.

Mandák, B., Pyšek, P. & Bímová, K. (2004) History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: a hybrid spreading faster than its parents. *Preslia*, **76**, 15–64.

Marais, C., van Wilgen, B.W. & Stevens, D. (2004) The clearing of invasive alien plants in South Africa: a preliminary assessment of costs and progress. *South African Journal of Science*, **100**, 97–103.

Pheloung, P.C. (1995) Determining the weed potential of new plant introductions to Australia. *Agriculture Protection Board Report*, West Australian Department of Agriculture, Perth, Western Australia.

Pheloung, P.C., Williams, P.A. & Halloy, S.R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management*, **57**, 239–251.

Pyšek, P. (2001) Past and future of predictions in plant invasions: a field test by time. *Diversity and Distributions*, **7**, 145–151.

Pyšek, P., Prach, K. & Šmilauer, P. (1995) Relating invasion success to plant traits: an analysis of the Czech alien flora. *Plant invasions: general aspects and special problems* (ed. by P. Pyšek, K. Prach, M. Rejmánek and M. Wade), pp. 39–60. SPB Academic Publishing, Amsterdam.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.

Pyšek, P., Sádlo, J. & Mandák, B. (2002) Catalogue of alien plants of the Czech Republic. *Preslia*, **74**, 97–186.

Reichard, S. (1997) *Invasive woody plant species in North America*. Compiled and verified by Sarah Reichard. University of Washington, Seattle, Washington.

Reichard, S.H. (2001) The search for patterns that enable invasion prediction. *Weed risk assessment* (ed. by R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 10–19. CSIRO Publishing, Melbourne, Australia.

Reichard, S.H. & Hamilton, C.W. (1997) Predicting invasions of woody plants introduced into North America. *Conservation Biology*, **11**, 193–203.

Rejmánek, M. (1996) A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, **78**, 171–181.

Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J. & Grotkopp, E. (2005a) Ecology of invasive plants — state of the art. *Invasive alien species: a new synthesis* (ed. by H.A. Mooney, R.N. Mack, J.A. McNeely, L. Neville, P.J. Schei and J. Waage), pp. 104–161. Island Press, Washington, D.C.

Rejmánek, M., Richardson, D.M. & Pyšek, P. (2005b) Plant invasions and invasibility of plant communities. *Vegetation ecology* (ed. by E. Van der Maarel), pp. 332–355. Blackwell Publishing, Oxford.

Richardson, D.M. (1998) Forestry trees as invasive aliens. *Conservation Biology*, **12**, 18–26.

Richardson, D.M., Binggeli, P. & Schroth, G. (2004a) Invasive agroforestry trees: problems and solutions. *Agroforestry and biodiversity conservation in tropical landscapes* (ed. by G. Schroth, D.A.B. De Fonseca, G.A. Harvey, C. Gascon, H.L. Vasconselos and A.-M. N. Izac), pp. 371–396. Island Press, Washington, D.C.

Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, (in press).

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.

Richardson, D.M. & Rejmánek, M. (2004) Invasive conifers: a global survey and predictive framework. *Diversity and Distributions*, **10**, 321–331.

Richardson, D.M., Rouget, M. & Rejmánek, M. (2004b) Using natural experiments in the study of alien tree invasions: opportunities and limitations. *Experimental approaches to conservation biology* (ed. by M.S. Gordon and S.M. Bartol), pp. 180–201. University of California Press, Berkeley.

Rouget, M. & Richardson, D.M. (2003) Understanding patterns of plant invasion at different spatial scales: quantifying the roles of environment and propagule pressure. *Invasions: ecological threats and management solutions* (ed. by L.E. Child, J.H. Brock, G. Brundu, K. Prach, P. Pyšek, P.M. Wade and M. Williamson), pp. 3–15. Backhuys Publishers, Leiden, the Netherlands.

Rouget, M., Richardson, D.M., Nel, J.L., Le Maitre, D.C., Egoh, B. & Mgidi, T. (2004) Mapping the potential ranges of major plant invaders in South Africa, Lesotho and Swaziland using climatic suitability. *Diversity and Distributions*, **10**, 475–484.

Sax, D.F. (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography*, **28**, 139–150.

Scott, J.K. & Panetta, F.D. (1993) Predicting the Australian weed status of southern African plants. *Journal of Biogeography*, **20**, 87–93.

Smith, C.S., Lonsdale, W.M. & Fortune, J. (1999) When to ignore advice: invasion predictions and decision theory. *Biological Invasions*, **1**, 89–96.

Svoboda, A.M. (1976) *The introduction of ornamental conifers*. Academia, Praha (In Czech).

Svoboda, A.M. (1981) *The introduction of ornamental hardwoods*. Academia, Praha (In Czech).

Tucker, K.C. & Richardson, D.M. (1995) An expert system for screening potentially invasive alien plants in South African fynbos. *Journal of Environmental Management*, **44**, 309–338.

Weber, E. (2003) *Invasive plant species of the world: a reference guide to environmental weeds*. CABI Publishing, Wallingford, UK.

Weber, E. & Gut, D. (2004) Assessing the risk of potentially invasive plant species in central Europe. *Journal for Nature Conservation*, **12**, 171–179.

Williamson, M. (1996) *Biological invasions*. Chapman & Hall, London.

Williamson, M. (1999) Invasions. *Ecography*, **22**, 5–12.

Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.

Windrlechner, M.P. (2001) The role of environmental analogs in identifying potentially invasive woody plants in Iowa. *Journal of Iowa Academy of Science*, **108**, 158–165.

Windrlechner, M.P. & Iles, J.K. (2002) A geographic assessment of the risk of naturalization of non-native woody plants in Iowa. *Journal of Environmental Horticulture*, **20**, 47–56.

Windrlechner, M.P., Thompson, J.R., Iles, J.K. & Dixon, P.M. (2004) Models for predicting the risk of naturalization of non-native woody plants in Iowa. *Journal of Environmental Horticulture*, **22**, 23–31.

SUPPLEMENTARY MATERIAL

The following material is available online at
http://www.blackwell-synergy.com/loi/ddi

Appendix S1 List of species used in the present study and results of their evaluation using the three tested prediction schemes.