Journal of
Plant Ecology

VOLUME 5, NUMBER 2,
PAGES 167–173

JUNE 2012

doi: 10.1093/jpe/rtr021

Advanced Access published
on 22 July 2011

available online at
www.jpe.oxfordjournals.org

Predicting plant invasiveness from native range size: clues from the Kashmir Himalaya

Manzoor A. Shah[1,]*, *Zafar A. Reshi*[1] *and Claude Lavoie*[2]

[1] *Department of Botany, University of Kashmir, Srinagar-190006, Jammu and Kashmir, India*
[2] *École supérieure d'aménagement du territoire et de développement régional, Université Laval, Quebec City, Quebec G1V 0A6, Canada*
*Correspondence address. Department of Botany, University of Kashmir, Srinagar-190006, Jammu and Kashmir, India. Tel: +9596-191292; Fax: +0194-2424735; E-mail: mashah75@yahoo.com

Abstract

Aims
In view of the growing interest in modelling the potential spread of invasive species, prediction of plant invasiveness on the basis of native range size holds considerable promise. Our objective was to use a simple model to evaluate whether a wider native range predisposes plant species to become invasive in non-native regions and to easily identify potential invaders on this basis. The Kashmir Himalayan alien flora, of which a large proportion is native to Europe, was used to test this model.

Methods
The Kashmir Himalayan alien flora comprises 436 species of vascular plants at different stages of invasion. We focussed on plant species at two critical invasion stages (*sensu* Colautti and MacIsaac 2004), i.e. Stage II (species that are just at the earliest phase of introduction) and Stage V (species that are widespread and dominant in the invaded region and are thus considered invasive). We used the territorial distribution in Europe (number of countries) as a surrogate for the native range size of plants of European origin.

Important Findings
Using a subset of 88 species, for which information on the native European range was available, we showed that a large proportion (68%) of Stage II species growing in the Kashmir Valley had a relatively restricted European range (present in ⩽20 countries); on the other hand, 77% of Stage V species had an extensive native range (present in >20 countries). We consequently hypothesized that 14 Kashmir Himalayan Stage II species of European origin that are distributed in >20 European countries are at risk of becoming future invaders in Kashmir. On the other hand, those Kashmir Himalayan Stage II species of European origin distributed in ⩽20 European countries are less likely to become invasive. Although this analysis is quite simple, the data suggest that a wider native range is a good predictor of plant invasiveness and could be used as a simple and low-cost early warning tool in predicting potential invasive species.

Keywords: Colautti and MacIsaac model • early warning system • Kashmir Himalaya • native range • plant invasion • prediction and management

Received: 28 January 2011 Revised: 28 May 2011 Accepted: 20 June 2011

INTRODUCTION

Rapid spread of invasive species beyond their home range is sometimes detrimental to native species and ecosystem functions in the introduced regions, potentially inflicting considerable socio-economic damages (Pimentel *et al.* 2005). More than 30 hypotheses (reviewed by Catford *et al.* 2009) have been proposed to explain species invasiveness and community invasibility. However, identifying potential invasive species in the introduced range still remains a challenge. Ecological niche modelling, in conjunction with climate matching and integrated phenomenological and mechanistic models (hybrid models), has been used to predict potential invasions (Drake and Bossenbroek 2004; Gallien *et al.* 2010; Hoffman 2001; Iguchi *et al.* 2004; Peterson and Vieglais 2001). Recently, a meta-analysis suggested that future plant invasions could possibly be predicted from species traits (van Kleunen *et al.* 2010). Thus, biological traits of species (Moravcová *et al.* 2010; Pyšek *et al.* 2009), together with propagule pressure (Simberloff 2009) and residence time (Pyšek and Jarošík

2005), may have a significant influence on invasiveness. These approaches are, however, incomplete since they do not take into account the size of the native range of the invaders. In fact, the likelihood of invasiveness can be effectively predicted on the basis of native range size (Herron *et al.* 2007; Pyšek *et al.* 2009; Rejmánek *et al.* 2003; Williamson 2001). Some studies have shown that species with extended native ranges have larger distributions in introduced regions than congeneric or confamilial species with smaller native ranges (Goodwin *et al.* 1999; Rejmánek 1996, 2000).

The alien vascular flora of the Kashmir Himalayan region was recently compiled and all the species were characterized on the basis of different invasion stages (Khuroo *et al.* 2008), in accordance with the model proposed by Colautti and MacIsaac (2004). The model characterizes different invasion stages on the basis of the abundance and distribution of alien species in the introduced range. Starting from resident species in a potential donor region (Stage 0), carried through different transport vectors (Stage I), and released into the introduced region (Stage II), the species may become localized and numerically rare (Stage III), widespread but rare (Stage IVa), localized but dominant (Stage IVb) or widespread and dominant (Stage V). Since Stage II species are at the initial stage of introduction and Stage V species are highly invasive, the former require a focus on timely prediction and early warning (and eventually eradication) and the latter need urgent and alternative management practices to prevent further spread or damage. We hypothesized that the Colautti and MacIsaac (2004) model can be used with data on the extent of native ranges to identify plant invaders. In the Kashmir Himalayan context, we evaluated whether or not a wider native range predisposes an alien species to be invasive.

METHODS

Study area

The Kashmir Himalayan region (from 32°20′ to 34°50′N and from 73°55′ to 75°35′E) includes parts of Pirpanjal range of Lesser Himalaya in the south and southwest and the Zanskar range of Greater Himalaya in the north and northeast. The region covers an area of 15 948 km^2, with a large altitudinal range of 1 600–5 420 m above sea level. The Kashmir Valley is a lacustrine basin located in an intermontane depression existing between the Lesser and the Greater Himalaya and contains numerous terrestrial and freshwater ecosystems. The valley experiences a temperate climate with relatively hot summers and moderate winters. The average maximum temperature fluctuates from 15 to 31°C, and the average minimum temperature ranges from −4 to 4°C. Annual precipitation totals 1 050 mm, about 70% of which occurs in the form of snow (Bhutiyani *et al.* 2007). Owing to its picturesque landscapes and scenic beauty, the Kashmir Valley is promoted as a tourist destination. This focus, together with a multifold increase in trade and transport over the years (by about 300 times since last century), has contributed significantly to the introduction and establishment of alien species and to the spread of a large number of invasive species (Khuroo *et al.* 2007).

Data sets and analysis

For the present study, we used a data set containing current invasion stages of alien plant species in the Kashmir Himalayan region (Khuroo *et al.* 2008), based on the Colautti and MacIsaac (2004) model. Most of the alien plant species (38%) in the Kashmir Himalaya are native to Europe, followed by Asia (27%), Africa (15%), North America (10%), South America (8%) and Australia (2%), respectively (Khuroo *et al.* 2007). The alien species have been categorized into different invasion stages on the basis of extent of spatial spread in the Kashmir Himalayan region, measured in terms of the frequency and percentage cover across study sites using 1, 5 and 10-m^2 quadrats for herbs, shrubs and trees, respectively (Khuroo *et al.* 2008).

We focussed on Stage II and Stage V species, which comprise about 45% of the total alien flora of the region because from a management perspective these stages represent two extreme and most critical stages of plant invasion. For the Kashmir Himalayan Stage II species, our aim was to identify potential invaders; for the Stage V species, we evaluated whether species with a wider native range were more widespread invaders. We also focussed on species from Europe because this continent is the dominant source of alien species for the Kashmir Himalayan flora (Khuroo *et al.* 2007). It was also because no reliable database on the distribution range was available for Asian and African species. Excellent databases exist for North American species (see the 'Invasive Plant Atlas of the United States': www.invasiveplantatlas.org, and the 'PLANTS Database': www.plants.usda.gov), but North American plants only represent a very small fraction of the total number of exotic species of the Kashmir Himalayan flora. Information about the distribution of alien species in their native European range was derived from the *Atlas Flora Europaeae* (Jalas *et al.* 1972–2004) and the *Flora Europaeae* (Tutin *et al.* 1968–2001). To estimate the distribution, we simply counted the number of countries in Europe where each species was present. We took into account the number of countries after the emergence of new political jurisdictions from the former Czechoslovakia, USSR and Yugoslavia. It should be noted that the European part of Russia was too large to be considered as a single unit; it was consequently subdivided into four territories (Northern division, Kalininigradskaya oblast, Central division and Southeastern division) as given in the *Atlas Flora Europaeae* (volumes 13, 14 and 15).

Species belonging to Stage II and Stage V (in Kashmir Himalaya) were categorized into four classes based on the extent of their territorial distribution in Europe (native range). In view of the total number of European countries (39, including Russian territories), we classified the species on the basis of their distribution into four classes (A, B, C and D), which included species present in 1–10, 11–20, 21–30 and 31–39 European countries, respectively. Although the territorial distribution

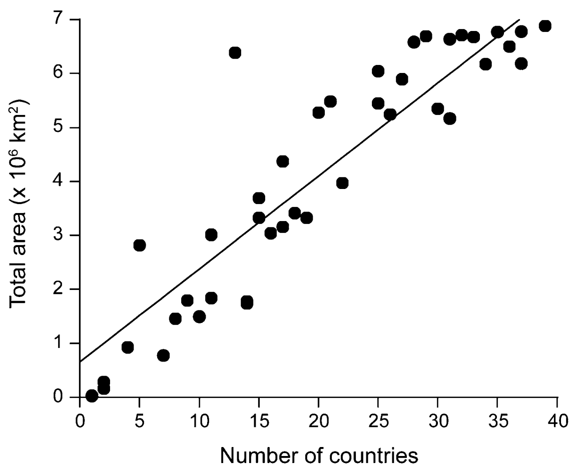

Figure 1: Relationship between the number of European countries with the presence of a vascular plant species and the total area calculated with the data from 88 European species that have been introduced in the Kashmir Himalayan region.

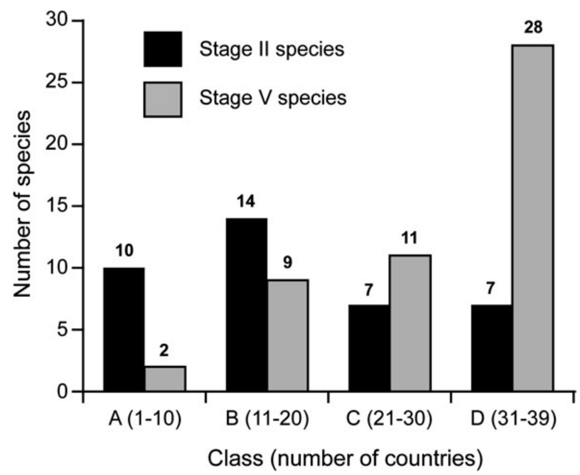

Figure 2: Number of European vascular plant species that have been introduced in the Kashmir Himalayan region according to their invasion stage. Black bars represent Stage II and grey bars Stage V species. Native distribution classes A, B, C and D represent the species occurrence in 1–10, 11–20, 21–30, and 31–39 European countries, respectively.

of species in Europe (number of countries) was taken as a surrogate for the extent of native distribution, we did take into account the variation in country size. The relationship between the number of countries and their total area was tested with the pool of species used in the analysis, to verify whether the number of countries was an effective surrogate for area. We also tested using χ^2 tests whether or not, for each stage (II and V), the distribution of the number of species into the different classes (A–D) significantly differed from a random distribution (Scherrer 1984).

RESULTS

Of the 436 alien plant species of the Kashmir Himalayan region at all invasion stages, we focussed on 196 species (51 families and 148 genera) that belonged to Stage II (119 species) and Stage V (77 species). These species represent about 45% of the alien flora of the region. Eighty-eight species belonging to Stages II and V were native to Europe (Appendix), which met our criteria for further analysis. Species that were not native to Europe or not described to date in the *Flora Europaeae* project were excluded. Species with no clearly known origin were also excluded.

A highly significant correlation ($R^2 = 0.851$; $P < 0.001$) was obtained between the number of European countries in which the species occurred (native range) and the total area of these countries for the 88 species used in the analysis (Fig. 1). The data revealed that most of the Stage II species (63%) could be categorized into the first two distribution classes (A and B), thereby indicating a restricted native range (Fig. 2). On the other hand, most Stage V species (78%) belonged to the last two distribution classes (C and D), thus reflecting a relatively wider native range. However, the distribution of the number of species into the different classes (A–D) significantly ($P < 0.05$) differed from a random distribution only for Stage V species. Species with a high risk of invasiveness in the near future include seven Stage II species with a wide native range (belonging to class D), specifically *Bidens tripartita* L., *Juncus inflexus* L., *Quercus robur* L., *Sagina procumbens* L., *Teucrium scordium* L., *Vicia sativa* L. and *Viola tricolor* L. In addition, seven Stage II species distributed in 21–30 European countries (class C) form a second group of potential invasive species. These include *Althaea officinalis* L., *Avena fatua* L., *Briza media* L., *Chenopodium opulifolium* Schd. ex DC., *Humulus lupulus* L., *Setaria pumila* Roem. and Schult. and *Trifolium dubium* Sibth.

DISCUSSION

Our simple analysis suggests that plant invasiveness in the Kashmir Himalayan region is at least partly influenced by the extent of the native range and that the number of European countries, easily obtainable information, can be used as a surrogate for native distribution. These results are in agreement with other studies (Goodwin *et al.* 1999; Pyšek *et al.* 2009; Rejmánek 1996, 2000), which also showed that species with a large native range have larger distributions in introduced regions than congeneric or confamilial species with a smaller native range. Species with a large native range are likely to become invasive because (i) similar traits, contributing to fitness and dispersal, allow a species to have a large range, whether native or exotic (Booth *et al.* 2003), (ii) broad native distribution is reflective of wide environmental tolerance, which is often correlated with invasiveness (Goodwin *et al.* 1999) and (iii) wide ranging species are more likely to be picked up and carried through different propagule transporting vectors (Forcella and Wood 1984; Roy 1990). The introduction of alien plants to

Kashmir Himalaya from European countries dates back to the early Aryans who invaded India about 1 500 BC (Chatterjee 1947). The process of introduction and transport of plant diaspores from Europe to this region was further exacerbated by the British colonial past of the Indian subcontinent.

Some outliers in our analysis have an extensive native range but are not yet successful invaders or have a small native range but are vigorous invaders. In these cases, analysis of biological traits (Milbau and Stout 2008; Moravcová *et al.* 2010; Pyšek *et al.* 2009; van Kleunen *et al.* 2010) or residence time (Gassó *et al.* 2010; Křivánek *et al.* 2006; Milbau and Stout 2008; Pyšek and Jarošík 2005) merits consideration. Other factors that could contribute to invasion success include chance events (Crawley 1989) and propagule pressure (Simberloff 2009), both in space (by widespread dissemination or abundant plantings) and time (by long history of cultivation; Bucharova and van Kleunen 2009; Dehnen-Schmutz *et al.* 2007; Hanspach *et al.* 2008; Křivánek *et al.* 2006; Pemberton and Liu 2009). The accuracy of predictive models for plant invasions could also be significantly improved by taking into account the taxonomic, biogeographical and biological characteristics of the species in the native range (van Kleunen *et al.* 2007). Besides species characteristics and native range size, the introduction history of the species has been found to be an important determinant of naturalization success of North American woody species in Europe (Bucharova and van Kleunen 2009).

The two stages of invasion we targeted are critical because species at Stage II, the earliest phase of introduction, are far easier to manage than the species that have already become widespread. While we predict that the seven Stage II species belonging to class D have the greatest invasiveness potential, we also suggest that the seven other Stage II species belonging to class C need special attention and monitoring. However, the precision of this prediction, based on a four-class grouping, is not perfect and is much better for Stage V species than for Stage II species, as suggested by the χ^2 tests. The precision would probably improve considerably if the time since introduction of these species was also considered. On the other hand, it is noteworthy that some of the Stage II—class D species that have been identified (*A.fatua*, *Q.robur*, *S.pumila*, *T.dubium* and *V.sativa*) are reportedly invasive in some North American states (see the *Invasive Plant Atlas of the United States*: www.invasiveplantatlas.org).

Several highly sophisticated and robust models have recently been proposed to predict the invasive potential of plant species (e.g. Broennimann and Guisan 2008; Gallien *et al.* 2010). Such models require large data sets, time of introduction or naturalization data and advanced statistical analyses that preclude ease of use, especially in the context of developing countries with relatively limited botanical expertise. Simpler models based on the distribution and abundance data of alien species in both the native and exotic ranges can be used as low-cost early warning tool in invasion management. The model we propose here is as effective as other widely used decision making tools; for instance, the *Australian Weed Risk Assessment System* can perform well in identifying weed species but can also have a high false-positive rate, rejecting 44% of non-weed species in Canada (McClay *et al.* 2010). In our particular case, we 'misclassified' (Stage II species in classes C and D, and Stage V species in classes A and B) 25 out of 88 species (28% of the total).

ACKNOWLEDGEMENTS

The research fellowship awarded to M.A.S. by the Department of Foreign Affairs and International Trade, Canada, under the Canadian Commonwealth Exchange Programme (Asia-Pacific) 2009 is gratefully acknowledged.

APPENDIX

List of alien vascular plant species from the Kashmir Himalayan region, along with their growth form, invasion stage (*sensu* Colautti and MacIsaac 2004) and country-wise distribution in their native European range, used in the predictive model of invasiveness

Family and species	Growth form[a]	Stage of invasion[b]	Number of countries (Europe)[c]
Alismataceae			
Alisma plantago-aquatica L.	Aq	V	35
Sagittaria sagittifolia L.	Aq	V	30
Amaranthaceae			
Amaranthus lividus L.	A	II	16
Apiaceae			
Daucus carota L.	B	V	35
Foeniculum vulgare Mill.	P	II	14
Asteraceae			
Anthemis cotula L.	B	V	35
Bidens tripartita L.	A	II	34
Chrysanthemum coronarium L.	P	II	11
Cirsium arvense Scop.	P	V	29
Silybum marianum Gaertn.	A	II	13
Brassicaceae			
Arabidopsis thaliana Heynh.	A	V	36
Capsella bursa-pastoris Medic.	A	V	39
Hesperis matronalis L.	B	II	14
Iberis amara L.	A	II	7
Lobularia maritima Desv.	A	II	10
Matthiola incana R. Br.	P	II	7
Sisymbrium loesellii L.	A	V	17
Butomaceae			
Butomus umbellatus L.	P	V	26
Cannabiaceae			
Cannabis sativa L.	A	V	1
Capparidaceae			

Table
Continued

Family and species	Growth form[a]	Stage of invasion[b]	Number of countries (Europe)[c]
Humulus lupulus L.	P	II	27
Caryophyllacaeae			
Arenaria serpyllifolia L.	A	V	36
Sagina procumbens L.	P	II	34
Stellaria media Cyr.	A	V	34
Ceratophyllaceae			
Ceratophyllum demersum L.	Aq	V	31
Chenopodiaceae			
Chenopodium album L.	A	V	36
Chenopodium foliosum Aschers.	P	V	9
Chenopodium opulifolium Schd. ex DC.	P	II	25
Convolvulaceae			
Convolvulus arvensis L.	P	V	37
Cuscutaceae			
Cuscuta planiflora Tenore	Ps	II	14
Cyperaceae			
Cyperus difformis L.	A	V	14
Cyperus rotundus L.	P	V	17
Euphorbiaceae			
Euphorbia helioscopia L.	A	V	36
Fabaceae			
Lathyrus odoratus L.	C	II	2
Medicago polymorpha L.	A	V	20
Trifolium dubium Sibth.	A	II	29
Trifolium pratense L.	P	V	36
Trifolium repens L.	P	V	39
Vicia narbonensis L.	A	II	15
Vicia sativa L.	A	II	37
Fagaceae			
Quercus robur L.	T	II	31
Iridaceae			
Iris spuria L.	P	II	11
Juncaceae			
Juncus articulatus L.	Aq	V	39
Juncus inflexus L.	P	II	32
Lamiaceae			
Mentha longifolia L.	P	V	25
Salvia officinalis L.	Ss	II	4
Teucrium scordium L.	B	II	32
Lemnaceae			
Lemna minor L.	Aq	V	37
Spirodela polyrhiza Schleid.	Aq	V	30
Malvaceae			
Althaea officinalis L.	P	II	27
Marsileaeceae			
Marsilea quadrifolia L.	Aq	V	17

Table
Continued

Family and species	Growth form[a]	Stage of invasion[b]	Number of countries (Europe)[c]
Menyanthaceae			
Nymphoides peltatum Kuntze	Aq	V	28
Nympheaceae			
Nymphaea lotus L.	Aq	II	1
Onagraceae			
Epilobium hirsutum L.	P	V	33
Oxalidaceae			
Oxalis corniculata L.	P	V	20
Papaveraceae			
Papaver macrostomum Boiss.	A	II	2
Papaver somniferum L.	A	II	8
Plantaginaceae			
Plantago lanceolata L.	P	V	39
Plantago major L.	P	V	39
Poaceae			
Agrostis stolonifera L.	P	V	39
Avena fatua L.	P	II	30
Briza media L.	P	II	28
Bromus inermis Leyss.	P	V	20
Dactylis glomerata L.	P	V	39
Lagurus ovatus L.	A	II	16
Lygeum spartum Loefl. ex L.	P	II	5
Phragmites australis Trin.	P	V	36
Poa annua L.	A	V	39
Polypogon monspeliensis Desf.	A	II	17
Setaria pumila Roem. and Schult.	A	II	22
Setaria viridis P. Beauv.	A	V	25
Vulpia myuros Gmel.	A	V	30
Polygonaceae			
Polygonum hydropiper L.	A	V	36
Polygonum maritimum L.	P	II	20
Potamogetonaceae			
Potamogeton crispus L. var. *serrulatus* Reichb.	Aq	V	33
Ranunculaceae			
Nigella damascena L.	A	II	15
Ranunculus arvensis L.	A	V	32
Ranunculus muricatus L.	A	V	17
Ranunculus sceleratus L.	A	V	33
Rosaceae			
Rubus ulmifolius Schott.	S	V	21
Sorbus domestica L.	T	II	15
Salicaceae			
Salix alba L.	T	V	21
Saliviniaceae			
Salvinia natans All.	Aq	V	18

Table
Continued

Family and species	Growth form[a]	Stage of invasion[b]	Number of countries (Europe)[c]
Scrophulariaceae			
Antirrhinum majus L.	A	II	5
Digitalis grandiflora Mill.	P	II	19
Trapaceae			
Trapa natans L.	Aq	V	21
Typhaceae			
Typha angustifolia L.	Aq	V	34
Urticaceae			
Urtica dioica L.	P	V	36
Violaceae			
Viola tricolor L.	A	II	31

Abbreviations: A = annual herb, Aq = aquatic plant, B = biennial herb, C = climber plant, P = perennial herb, Ps = parasitic herb, S = shrub, Ss = subshrub, T = tree.
[a]According to Khuroo *et al.* (2007).
[b]According to Khuroo *et al.* (2008).
[c]According to Tutin *et al.* (1968–2001) and Jalas *et al.* (1972–2004).

REFERENCES

Bhutiyani MR, Kale VS, Pawar NJ (2007) Long-term trends in maximum, minimum and mean air temperatures across the Northwestern Himalaya during the twentieth century. *Clim Change* **85**:159–77.

Booth BD, Murphy SD, Swanton CJ (2003) *Weed Ecology in Natural and Agricultural Systems*. Wallingford, UK: CABI Publishing.

Broennimann O, Guisan A (2008) Predicting current and future biological invasions: both native and invaded ranges matter. *Biol Lett* **4**:585–9.

Bucharova A, van Kleunen M (2009) Introduction history and species characteristics partly explain naturalization success of North American woody species in Europe. *J Ecol* **97**:230–8.

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers Distrib* **15**:22–40.

Chatterjee D (1947) Influence of east Mediterranean region flora on that of India. *Sci Cult* **13**:9–11.

Colautti RI, MacIsaac HJ (2004) A neutral terminology to define 'invasive' species. *Divers Distrib* **10**:135–41.

Crawley MJ (1989) Chance and timing in biological invasions. In Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M, Williamson M (eds). *Biological Invasions: A Global Perspective*. Chichester, UK: Wiley, 407–24.

Dehnen-Schmutz K, Touza J, Perrings C, *et al.* (2007) The horticultural trade and ornamental plant invasions in Britain. *Conserv Biol* **21**:224–31.

Drake JM, Bossenbroek JM (2004) The potential distribution of zebra mussels in the United States. *Bioscience* **54**:931–41.

Forcella F, Wood JT (1984) Colonization potentials of alien weeds are related to their native distributions: implications for plant quarantine. *J Aust Inst Agric Sci* **50**:35–41.

Gallien L, Munkemuller T, Albert CH, *et al.* (2010) Predicting potential distributions of invasive species: where to go from here? *Divers Distrib* **16**:331–42.

Gassó N, Basnou C, Vilà M (2010) Predicting plant invaders in the Mediterranean through a weed risk assessment system. *Biol Invasions* **12**:463–76.

Goodwin BJ, McAllister AJ, Fahrig L (1999) Predicting invasiveness of plant species based on biological information. *Conserv Biol* **13**:422–6.

Hanspach J, Kühn I, Pyšek P, *et al.* (2008) Correlates of naturalization and occupancy of introduced ornamentals in Germany. *Perspect Plant Ecol* **10**:241–50.

Herron PM, Martine C, Latimer AM, *et al.* (2007) Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. *Divers Distrib* **13**:633–44.

Hoffmann MH (2001) The distribution of *Senecio vulgaris*: capacity of climatic range models for predicting adventitious ranges. *Flora* **196**:395–403.

Iguchi K, Matsuura K, McNyset K, *et al.* (2004) Predicting invasions of North American basses in Japan using native range data and a genetic algorithm. *Trans Am Fish Soc* **133**:845–54.

Jalas J, Suominen J, Lampinen R, Kurtto A, Junikka L, Fröhner SE, Weber HE, Sennikov AN (eds). (1972–2004) Atlas Florae Europaeae. Distribution of Vascular Plants in Europe, Vol. I–XIV. Helsinki, Finland: Committee for mapping the flora of Europe and Societas Biologica Fennica Vanamo.

Khuroo AA, Rashid I, Reshi Z, *et al.* (2007) The alien flora of Kashmir Himalaya. *Biol Invasions* **9**:269–92.

Khuroo AA, Reshi Z, Rashid I, *et al.* (2008) Operational characterization of alien invasive flora and its management implications. *Biodivers Conserv* **17**:3181–94.

Křivánek M, Pyšek P, Jarošík V (2006) Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. *Conserv Biol* **20**:1487–98.

McClay A, Sissons A, Wilson C, *et al.* (2010) Evaluation of the Australian weed risk assessment system for the prediction of plant invasiveness in Canada. *Biol Invasions* **12**:4085–98.

Milbau A, Stout JC (2008) Factors associated with alien plants transitioning from casual, to naturalized, to invasive. *Conserv Biol* **22**:308–17.

Moravcová L, Pyšek P, Jarošík V, *et al.* (2010) Reproductive characteristics of neophytes in the Czech Republic: traits of invasive and non-invasive species. *Preslia* **82**:365–90.

Pemberton RW, Liu H (2009) Marketing time predicts naturalization of horticultural plants. *Ecology* **90**:69–80.

Peterson AT, Vieglais DA (2001) Predicting species invasions using ecological niche modeling: new approaches from bioinformatics attack a pressing problem. *Bioscience* **51**:363–71.

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econ* **52**:273–88.

Pyšek P, Jarošík V (2005) Residence time determines the distribution of alien plants. In Inderjit (ed). *Invasive Plants: Ecological and Agricultural Aspects*. Basel, Germany: Birkhäuser Verlag-AG, 77–96.

Pyšek P, Jarošík V, Pergl J, *et al.* (2009) The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Divers Distrib* **15**:891–903.

Rejmánek M (1996) A theory of seed plant invasiveness: the first sketch. *Biol Conserv* **78**:171–81.

Rejmánek M (2000) Invasive plants: approaches and predictions. *Austral Ecol* **25**:497–506.

Rejmánek M, Richardson DM, Higgins SI, *et al.* (2003) Ecology of invasive plants: state of the art. In Mooney HA, McNeely JA, Neville L, Schei PJ, Waage JK (eds). *Invasive Alien Species: Searching for Solutions*. Washington, DC: Island Press, 104–61.

Roy J (1990) In search of the characteristics of plant invaders. In: di Castri F, Hansen AJ, Debussche M (eds). *Biological Invasions in Europe and Mediterranean Basin*. Dordrecht, The Netherlands: Kluwer Academic Publishers, 335–52.

Scherrer B (1984) *Biostatistique*. Québec, Canada: Gaëtan Morin.

Simberloff D (2009) The role of propagule pressure in biological invasions. *Annu Rev Ecol Evol Syst* **40**:81–102.

Tutin TG, Heywood VH, Burges NA, *et al.* (1968–2001) *Flora Europaeae*. Vol. I–V. Cambridge, UK: Cambridge University Press.

van Kleunen M, Johnson SD, Fischer M (2007) Predicting naturalization of southern African Iridaceae in other regions. *J Appl Ecol* **44**:594–603.

van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol Lett* **13**:235–45.

Williamson M (2001) Can the impacts of invasive plants be predicted? In Brundu G, Brock JH, Camarda I, Child LE, Wade M (eds). *Plant Invasions: Species, Ecology and Ecosystem Management*. Leiden, The Netherlands: Backhuys Publishers, 11–9.