



Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England

Patrick M. Herron^{1*}, Christopher T. Martine², Andrew M. Latimer¹ and Stacey A. Leicht-Young³

¹Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Storrs, CT 06269-3043, USA,

²Department of Biological Sciences, Plattsburgh State University of New York, 101 Broad Street, Plattsburgh, NY 12901, USA, ³Lake Michigan Ecological Research Station, USGS Great Lakes Science Center, 1100 North Mineral Springs Road, Porter, IN 46304, USA

*Correspondence: Patrick M. Herron, Department of Ecology and Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Storrs, CT 06269-3043, USA. Tel.: 011 (860) 486 5382; Fax: 011 (860) 486 6364; E-mail: patrickherron12@gmail.com

ABSTRACT

Effective management of introduced species requires the early identification of species that pose a significant threat of becoming invasive. To better understand the invasive ecology of species in New England, USA, we compiled a character data set with which to compare non-native species that are known invaders to non-native species that are not currently known to be invasive. In contrast to previous biological trait-based models, we employed a Bayesian hierarchical analysis to identify sets of plant traits associated with invasiveness for each of three growth forms (vines, shrubs, and trees). The resulting models identify a suite of 'invasive traits' highlighting the ecology associated with invasiveness for each of three growth forms. The most effective predictors of invasiveness that emerged from our model were 'invasive elsewhere', 'fast growth rate', 'native latitudinal range', and 'growth form'. The contrast among growth forms was pronounced. For example, 'wind dispersal' was positively correlated with invasiveness in trees, but negatively correlated in shrubs and vines. The predictive model was able to correctly classify invasive plants 67% of the time (22/33), and non-invasive plants 95% of the time (204/215). A number of potential future invasive species in New England that deserve management consideration were identified.

Keywords

Bayesian, biological invasions, dispersal, invasive species, latitudinal range, life history, plant ecology, shade tolerance.

INTRODUCTION

Invasive plants can alter plant community structure and ecosystem function (Vitousek *et al.*, 1987), result in large economic costs from lost ecosystem services (Pimentel *et al.*, 2005), and detract from an intrinsic or aesthetic value associated with native biodiversity and native plant dominance. The threat posed by non-native invasive plant species has spurred efforts to identify individual species that show a high probability for naturalization and/or invasiveness and to rapidly eradicate those species while their distributions are limited or prevent their introduction. Identifying suites of plant traits and corresponding ecological strategies used by successful invaders would improve our understanding of how particular species and landscape features interact to produce the explosive spread of invasive species.

Accurate assessment of the invasive potential of an introduced species before introduction would provide a valuable tool to reduce invasions. This is particularly true in the USA, where a majority of invasive plants are introduced intentionally by the agriculture, forestry, and nursery trades (Reichard & White,

2001; Mack & Erneberg, 2002), and thus it may be possible to control introductions in the future. Treating the past introductions of hundreds of woody exotic plants into New England as a 'natural experiment' in biogeography, we use statistical models to explore the ecology of woody plant invasions, test their predictive ability, and identify species that may pose future threats. The problems associated with invasive plants are conspicuous in the New England states where an estimated 877 non-native plant species have become established, comprising 31% of the flora (Rejmánek & Randall, 1994).

Significant effort in the last 20 years has been spent on determining the correlation between life-history traits and invasiveness (see Pyšek & Richardson (2007) for a review). Correlates of invasive success recorded in the literature for plants include short juvenile period and interval between seed crops (Richardson & Rejmánek, 2004), high relative growth rate (Grotkopp *et al.*, 1998; Pattison *et al.*, 1998; Grotkopp *et al.*, 2002), long flowering period (Goodwin *et al.*, 1999; Cadotte & Lovett-Doust, 2001; Pyšek *et al.*, 2003; Lloret *et al.*, 2005), vertebrate seed dispersal (Binggeli, 1996; Rejmánek & Richardson, 1996; Rejmánek,

1996a; Richardson *et al.*, 2000), and vegetative reproduction (Auld *et al.*, 1983; Horak *et al.*, 1987; Henderson, 1991). Some traits expected to be correlated with invasiveness in multispecies comparisons have yielded ambiguous or non-significant results across studies (e.g. seed size; Pyšek *et al.*, 2003; Lloret *et al.*, 2005; Pyšek & Jarošík, 2005; Cadotte *et al.*, 2006; but see Hamilton *et al.*, 2005). Even traits that are considered among the strongest predictors from multiple studies are found to be non-significant in many others. The inconsistency among these studies of biological traits certainly arises in part from differences in sample sizes, stage of invasion examined (Perrings *et al.*, 2005), and the role of other components of invasion biology that are more difficult to measure: stochastic factors (propagule pressure, residence time, and chance events) (Rejmánek *et al.*, 2005) and community invasibility (Lonsdale, 1999).

Yet, despite the lack of agreement between all of these studies on a coherent set of biological traits, in general these studies seem to be converging (Kolar & Lodge, 2001) on a number of important biological traits associated with invasion in vascular plants: plant height, vigorous vegetative growth, long flowering period, and attractiveness to humans (Pyšek & Richardson, 2007). In addition, although not intrinsic biological traits, history of invasion elsewhere (Scott & Panetta, 1993; Williamson & Fitter, 1996; Reichard & Hamilton, 1997) and size of native range of a species (Forcella & Wood, 1984; Rejmánek, 1995, 1996b, 1999; Goodwin *et al.*, 1999) are the most consistent predictors of invasive success of plants.

A number of the previous studies listed above have built predictive models of invasiveness by identifying life-history traits of known non-native naturalized or invasive plants and comparing them with the traits of either the local native flora, or the introduced non-naturalized or non-invasive flora (Scott & Panetta, 1993; Rejmánek & Richardson, 1996; Williamson & Fitter, 1996; Reichard & Hamilton, 1997; Goodwin *et al.*, 1999; Frappier & Eckert, 2003). In terms of predictive ability, these previous retrospective models correctly identified invasive plants at rates of between 70% and 90%, but demonstrate 'low positive predictive value' (see Smith *et al.*, 1999; Hughes & Madden, 2003; Caley *et al.*, 2006 for discussions of this topic). While these models may be better explanatory devices than predictive tools (see Smith *et al.*, 1999; Pyšek *et al.*, 2004), these efforts are important steps towards an understanding of plant invasion, hypothesis generation, and the development of screening programmes. Notwithstanding the discrepancies that arise in comparing analyses of plants from different geographical regions, most of these analyses found traits that were correlated with invasion success. This implies that these traits have a strong influence on the probability of being invasive and are partly tied to the properties of the invaded ecosystem. Studying the characteristics of exotic plants that have become invasive thus can potentially provide valuable insights into the ecology of colonization, the interaction of colonization and disturbance, and also make useful predictions about which species are likely to become successful future invaders.

This study combines a narrow geographical focus — the New England region of the north-eastern USA — with a wide species

focus. This narrow geographical focus, along with our concentration on woody perennial plants, facilitates interpretation of model results in terms of ecological strategy and relationships to disturbance and land-use history. The backbone of this model is a large species data set (encompassing 54 families and 248 species) that enables robust statistical tests of trait associations, as well as the detection of trait associations that vary across growth forms. Together, these design elements allow this study to provide ecological interpretations while attaining generality and predictive power characteristic of more broadly focused studies (e.g. Reichard & Hamilton, 1997).

Methodologically, our approach is unique in that it uses a Bayesian hierarchical model to explore whether there are multiple discrete sets of invasive traits that confer invasive success on non-native plants in a single region. Its major strength is in striking a balance between flexibility — accommodating differences among subgroups of species — and generality — overfitting the data by over-parameterization (Gelman *et al.*, 1995; Congdon, 2003). The statistical methodology employed here and the models we have developed can be applied directly to other regions.

Our results provide further support for some of the conclusions emerging collectively from previous studies: that there are particular traits that are linked to invasiveness across lineages and geographical regions, yet also that distinct invasive life-history traits are associated to different regions and different functional types or growth forms. Additionally, this study provides further evidence that invasive history is a very useful predictor of invasive success. This implies that there are attributes that are difficult to quantify through standard life-history traits yet endow some species with a relatively general invasive propensity.

METHODS

Data sources and preparation

A set of 248 exotic woody plant species was analysed using life-history traits, biogeographical information, habitat preference, and invasion history. This list included 33 species classified *a priori* as invasive in New England (~163,000 km² land). Species were classified as invasive in our data set based on two criteria: (1) listing of the species by the Invasive Plant Atlas of New England (IPANE) (Mehrhoff *et al.*, 2003), and (2) meeting the criteria for the definition of invasive plant species as described in Richardson *et al.* (2000) that defines standards for the rate of spread in the landscape. We included only species for which there is solid evidence of introduction and cultivation in New England as provided by Gleason & Cronquist (1991), the PLANTS database (<http://plants.usda.gov>), Dirr (1997), and Rehder (1940). The compiled list of species is representative of the diversity of plant families (54 families) and growth forms (shrubs, woody vines, and trees) among introduced woody species in the region.

Each of the selected species was coded for 28 characters considered relevant to their capability to naturalize in New England (Table 1, see Appendix S1 in Supplementary Material). Emphasis was placed on traits that characterize reproductive strategy, dispersal ability, growth rate, and tolerance along major

Table 1 List of characters for which data were scored for use in logistic regression, and Bayesian analyses.

Character	Character state
Growth form	Shrub, vine, tree
Evergreen or deciduous	Deciduous, semi-evergreen, evergreen
Growth rate	Slow, medium, fast
Cosexual/dioecious (sexual system)	Monoecious/hermaphrodite, dioecious
Shade tolerance	Yes, no
Vegetative reproduction	Yes, no
Known hybrids	Yes, no
Seed dispersal	Wind, bird, other animal, water, and passive
Flowering season	Spring, late spring, summer, late summer, fall, late fall, winter
Fruit maturity	Spring, late spring, summer, late summer, fall, late fall, winter
Fruit size	Inches (0–0.25, 0.26–0.99, 1 or greater)
Fleshy fruit	Yes, no
Seeds per fruit	1–2, 3–6, 7 or greater
Seed size	< 2 mm, < 5 mm, < 1 cm, ≥ 1 cm
Scarification required	Yes, no
Cold stratification required	Yes, no
Soil pH	< 5, 5–7, > 7
Soil moisture	Moist, well drained, dry, all/unknown
Hardiness zone min	1–10
Hardiness zone max	1–10
Native latitudinal range	log[degrees]
Native longitudinal range	log[degrees]
Native to North America	Yes, no
Susceptible to pests or pathogens	Yes, no
Naturalized elsewhere	Yes, no
Invasive elsewhere	Yes, no
Congeneric invasive	Yes, no
Confamilial invasive	Yes, no

environmental gradients (temperature, soil moisture, and light availability). Geographical and morphological character data were collected from an extensive set of references, including floristic treatments (Tutin *et al.*, 1964; Radford *et al.*, 1968; Gleason & Cronquist, 1991; Flora of North America Editorial Committee, 1993+; Komarov *et al.*, 1968–2002; Rhoads & Block, 2000; Miller, 2003); horticultural manuals (Rehder, 1940; Bailey, 1949; Young & Young, 1992; Dirr, 1997, 1998, 2002), and web resources (Brooklyn Botanic Garden, 2004; Flora of China Editorial Committee, 1994+; International Plant Names Index, <http://www.ipni.org>; PLANTS database). Information on the susceptibility to pathogens was collected from these same resources as listed above and reflects susceptibility in North America, rather than the native range. Data for some species were directly measured from herbarium specimens [from the George Safford Torrey Herbarium (CONN)] and living material (from the University of Connecticut's Ecology and Evolutionary Biology Conservatory and the University's Arboretum). These resources, combined with information provided by the Invasive Plant Atlas of New England (Mehrhoff *et al.*, 2003), were used to determine if a given species is a member of a genus or family that includes known invasives. Genus-level taxonomy is based on the Integrated Taxonomic Information System (<http://www.itis.usda.gov>). Family level taxonomy reflects the classification scheme of Judd *et al.* (2002).

The character trait 'invasive elsewhere' was coded for individual species based on whether they appear on state, national (e.g. PLANTS database), and international lists of invasive plants (e.g. ISSG Global Invasive Species Database, <http://www.issg.org/database>) covering regions other than the six New England states. We also relied on *A Global Compendium of Weeds* by Rod Randall and *Invasive Species of the World* by Ewald Weber (Randall, 2002; Weber, 2003).

We segregated the non-invasive species into two groups: species for which there is evidence of introduction and frequent use prior to 1900 in New England (Favretti & Favretti, 1990; Adams, 2004) and species that have been introduced more recently. The fact that introduced species may require substantial time and repeated introduction to become established (Kowarik, 1995; Crooks & Soulé, 1996) means there is substantial uncertainty about the potential invasiveness of recent introductions. Accordingly, the 83 species (all defined as non-invasive) introduced after 1900 were not used to fit any of the models. Models were fitted using the remaining 165 species that have been in New England for more than a century (33 invasive, 132 non-invasive). The resulting models were then used to predict the invasive potential of the more recent introductions.

In the language of Hamilton *et al.* (2005), the methodology of this study is a 'target-area' approach that compares invasion

success of a pool of species that are present and alien to the region. Thus any attributes the models identify as correlated with invasion are biased towards the post-introduction phase of invasion.

Statistical analysis

We used Bayesian logistic regression models in two separate analyses to relate the response variable (observed invasiveness) to the explanatory variables (species traits). In the first analysis (the 'predictive model'), we attempted to derive the strongest predictive model by including the variable 'invasive elsewhere' in the analysis. In the second analysis (the 'traits model'), we omitted the strong predictor 'invasive elsewhere' to assess which intrinsic plant traits would best correlate with invasive success in New England.

We employed stepwise logistic regressions in R 2.3.1 (R Development Core Team, 2006) and used the Akaike Information Criterion (AIC) to compare models as an exploratory tool to identify variables to test formally for inclusion in the Bayesian analyses (Venables & Ripley, 2002). This smaller set of variables were then included in a series of Bayesian models, with each variable removed one-by-one to determine whether removal of the variable resulted in a significantly weaker model as measured by the Deviance Information Criterion (DIC), a measure of model performance that penalizes models for complexity (Spiegelhalter *et al.*, 2002). In addition to testing for inclusion, we also ran models in which slopes for each variable were allowed to vary by growth form (shrub, tree, and vine). Growth-form-specific slopes were included if they improved model performance as measured by the DIC score. These steps were repeated for the analysis that did not include 'invasive elsewhere'.

The Bayesian logistic regressions were implemented in OPENBUGS version 2.2.0 (Thomas *et al.*, 2006). Code for the models is included in Appendix S2 in Supplementary Material. To allow the explanatory variables to take on different slopes for each plant growth form, we included random effects for each growth form, so that the slope for each growth form was the sum of an overall regression coefficient and the growth form random effect (see Appendix S2). Because we believed the responses of the different growth forms might be related to each other, we placed a multivariate normal prior on the random effects. This provided the model with the flexibility to allow the slopes for different growth forms to strongly influence each other, i.e. to allow the model to 'borrow strength' across growth forms — or to allow them to vary nearly independently (Congdon, 2003). In addition to testing variables and random effects for inclusion using DIC, we also reported whether the variables were significant in the sense that their credible intervals (the portion of the posterior distribution falling between the 0.025 and 0.975 quantiles) excluded 0 (Gelman *et al.*, 1995).

We assessed performance across all models by assessing false-positive and false-negative predictions. A threshold of 0.5 was used for the parameter p_i , which represents the probability that species i is invasive. If an individual plant i received a score of 0.5 or greater, the plant was predicted to be invasive. In addition to scoring how well the models fitted the data, cross-validation

Table 2 Predictor variables and coefficients for Bayesian hierarchical logistic regression for (a) 'predictive' model (all predictive variables) and (b) 'traits' model (without invasive elsewhere). The mean and standard deviation of the posterior distribution for each variable are reported. In addition, the 0.025 and 0.975 quantiles of the distribution are provided, and define the 95% credible interval for each coefficient. Bold variables indicate significant predictors.

(a)

Predictor variable	Mean	SD	0.025	0.975
Intercept	-6.777	1.175	-10.42	-3.502
Invasive elsewhere	3.724	0.983	2.053	5.92
Vine	-1.687	1.594	-4.990	1.380
Tree	-5.072	1.364	-8.068	-2.594
Wind dispersed	-0.872	2.239	-5.647	3.175
Native latitudinal range [log]	1.373	0.539	0.407	2.505
Shade tolerant	0.609	1.886	-2.984	4.386
Evergreen	-4.965	2.293	-10.62	-1.604
Semi-evergreen	0.692	1.752	-2.704	4.000
Tree * wind dispersal	3.462	2.371	-0.787	8.529
Shrub * wind dispersal	-1.89	3.688	-9.784	4.121
Vine * wind dispersal	-2.992	3.976	-11	8.529
Tree * shade tolerant	1.323	1.998	-2.704	5.184
Shrub * shade tolerant	-0.851	1.955	-4.788	2.898
Vine * shade tolerant	-0.011	2.182	-4.325	4.305

(b)

Predictor variable	Mean	SD	0.025	0.975
Intercept	-5.303	1.455	-8.353	-2.622
Vine	-0.305	0.775	-1.854	1.179
Tree	-3.076	0.927	-5.101	-1.478
Native latitudinal range [log]	1.455	0.489	0.527	2.443
Evergreen	-4.624	2.124	-9.743	-1.515
Fast growth rate	1.352	0.503	0.381	2.309
Wind dispersed	-1.291	2.062	-5.409	2.739
Tree * wind dispersal	3.468	2.161	-0.684	7.68
Shrub * wind dispersal	-3.232	5.021	-16.09	2.776
Vine * wind dispersal	-3.772	4.742	-13.38	2.196

was performed by holding out one data point at a time and refitting models on the remaining data to predict the omitted species.

RESULTS

Variable selection by stepwise logistic regression for the 'predictive' model, which has the variable 'invasive elsewhere' included, resulted in nine characters being chosen of 28 for testing in Bayesian models: 'evergreen', 'invasive elsewhere', 'native latitudinal range', 'shade tolerance', 'growth form [tree]', 'growth form [vine]', and 'vegetative reproduction'. After testing each of these characters in Bayesian models and comparing model performance (DIC score), eight of the variables and six interaction terms were included in the model (Table 2a). Some variables that

Table 3 Prediction rates of the 'predictive' model with and without cross-validation performed as part of the analysis.

	Bayesian (fit)	Bayesian (CV)	Bayesian (All species)
No. of invasive species in analysis	33	33	33
No. of non-invasive species in analysis	132	132	215
Percent	Invasive: 82%	67%	67%
Correct	Non-invasive: 95%	93%	95%
	Total: 92%	88%	91%

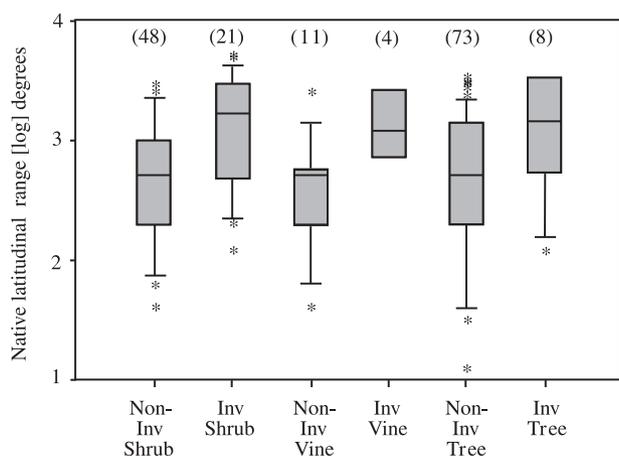


Figure 1 Comparison of native latitudinal range for both the invasive and the non-invasive species of each of the growth forms. The horizontal lines of the box plot denote the 25th, 50th, and 75th percentile values, while the whiskers represent the range of values. The asterisks above and below the whiskers denote outliers. The number above each of the boxes represents the number of species that contributed to the statistic.

we expected *a priori* to be important were in fact not selected, including soil moisture preference, ability to spread with vegetative growth, sexual system (co-sexual or dioecious), and whether the species is native elsewhere in North America.

In the 'predictive' model, 'invasive elsewhere' and 'native latitudinal range' (Fig. 1) were the only two variables with significantly positive coefficients, whereas the characters 'evergreen' and 'growth form [tree]' were both significantly negative coefficients. The only other variable associated with invasiveness (i.e. positive coefficient) that improved the model was 'shade tolerance'. The two other characters with non-significant negative coefficients were 'wind dispersal' and 'growth form [vine]'. All characters included in the model were tested with random effects for growth form — i.e. a test for heterogeneity of slopes across growth forms — to determine whether their inclusion significantly improved model performance (as measured by DIC). Growth form random effects for 'wind dispersal' significantly improved model performance. There was a strong contrast among growth forms, with 'wind dispersal' positively correlated with invasiveness in trees, but negatively correlated in shrubs and vines. In addition, there was a slight improvement in the model when growth form random effects were included to allow slopes to

vary for shade tolerance. Shade tolerance had no association with invasiveness for shrubs or vines, but had a weakly positive association in trees (credible interval of $\{-2.7, 5.2\}$).

The 'predictive' model without cross-validation correctly classified invasive plants 82% of the time (27/33), non-invasive plants 95% of the time (125/132), and all plants 90% of the time (152/165) (Table 3). Using hold-one-out cross-validation, the model correctly classified invasive plants 67% of the time (22/33), non-invasive plants 93% of the time (123/132), and all plants 88% of the time (145/165) (Table 3). When the 83 recently introduced species were also included, the model successfully discriminated between invasive and non-invasive plant species 90% of the time (226/248) (Table 3). The model was most successful identifying known invasive shrubs, correctly identifying 81% (17/21), followed by trees at 63% (5/8). The model was not able to classify any of the four invasive vines as invasive.

After cross-validation, the 'predictive' model produced a list of 11 missed invasives (false-negatives) and 11 non-invasives classified as invasives (false-positives) (Table 4, Fig. 2). When only model fit was considered (i.e. all data were included and all species were fit), the model committed fewer errors, with *Robinia pseudoacacia*, *Hypericum prolificum*, *Populus alba*, *Euonymus alatus*, *Ampelopsis brevipedunculata*, and *Acer ginnala* dropping out as missed invasives. Non-invasive plants incorrectly identified as invasive included *Euonymus europaeus*, *Tamarix ramosissima*, *Viburnum opulus*, *Viburnum lantana*, *Ligustrum amurense*, *Spiraea japonica*, and *Caragana arborescens*. With cross-validation and inclusion of the 83 recently introduced species excluded from the model fitting, four additional plants were identified as 'false positives': *Halimodendron halodendron*, *Rubus armeniacus*, *Ampelopsis aconitifolia*, and *Polygonum aubertii*.

In the 'trait' model, which had the variable 'invasive elsewhere' removed, the model identified the following variables as significant: 'native latitudinal range' (positive, Fig. 1), 'growth rate [fast]' (positive), 'evergreen' (negative), and 'growth form [tree]' (negative) (Table 2b). Variables included in the 'trait' model that were not statistically significant were 'growth form [vine]' (negative) and 'wind dispersal' (negative). The interaction term of 'wind dispersal' on 'growth form' was included for all growth forms and was positive for trees but negative for both vines and shrubs.

DISCUSSION

Despite the complexity of the original data set — 28 traits scored for 248 exotic woody species — our analysis produced simple,

Species	Fit	Standard deviation
Correctly classified invasives:		
<i>Cytisus scoparius</i> (L.) Link	0.838	0.111
<i>Frangula alnus</i> Mill.	0.836	0.082
<i>Rosa rugosa</i> Thunb.	0.812	0.119
<i>Berberis vulgaris</i> L.	0.804	0.087
<i>Ligustrum vulgare</i> L.	0.800	0.801
<i>Ligustrum sinense</i> Lour.	0.793	0.088
<i>Elaeagnus umbellata</i> Thunb	0.792	0.129
<i>Ligustrum obtusifolium</i> Sieb. & Zucc.	0.760	0.092
<i>Lonicera maackii</i> (Rupr.) Herder	0.751	0.092
<i>Lonicera morrowii</i> A. Gray	0.740	0.093
<i>Lonicera xylosteum</i> L.	0.730	0.098
<i>Acer pseudoplatanus</i> L.	0.727	0.154
<i>Acer platanoides</i> L.	0.720	0.160
<i>Alnus glutinosa</i> (L.) Gaertner	0.718	0.156
<i>Rhamnus cathartica</i> L.	0.707	0.096
<i>Ailanthus altissima</i> (Mill.) Swingle	0.659	0.163
<i>Ligustrum ovalifolium</i> Hassk.	0.622	0.110
<i>Rosa multiflora</i> Thunb. ex Murray	0.600	0.109
<i>Lonicera tatarica</i> L.	0.596	0.109
<i>Berberis thunbergii</i> DC.	0.574	0.111
<i>Amorpha fruticosa</i> L.	0.557	0.116
<i>Paulownia tomentosa</i> (Thunb.) Sieb. & Zucc.	0.550	0.170
False negatives: species known to be invasive, incorrectly classified as non-invasive.		
<i>Rubus phoenicolasius</i> Maxim.	0.488	0.170
<i>Celastrus orbiculatus</i> Thunb.	0.462	0.206
<i>Elaeagnus angustifolia</i> L.	0.452	0.169
<i>Lonicera japonica</i> Thunb.	0.417	0.193
<i>Acer ginnala</i> Maxim.	0.378	0.171
<i>Euonymus alatus</i> (Thunb.) Sieb.	0.335	0.138
<i>Ampelopsis brevipedunculata</i> (Maxim.) Trautv.	0.311	0.170
<i>Pueraria montana</i> (Lour.) Merr.	0.275	0.257
<i>Populus alba</i> L.	0.145	0.104
<i>Hypericum prolificum</i> L.	0.022	0.029
<i>Robinia pseudoacacia</i> L.	0.002	0.004
Potential new invaders		
<i>Euonymus europaeus</i> L.	0.836	0.080
<i>Tamarix ramosissima</i> Ledeb.	0.792	0.120
<i>Viburnum opulus</i> L. var. <i>opulus</i>	0.721	0.092
<i>Viburnum lantana</i> L.	0.716	0.145
<i>Halimodendron halodendron</i> (L. f.) Voss.	0.695	0.144
<i>Ligustrum amurense</i> Carr.	0.656	0.107
<i>Caragana arborescens</i> Lam.	0.607	0.171
<i>Spiraea japonica</i> L. f.	0.605	0.114
<i>Colutea arborescens</i> L.	0.546	0.303
<i>Rubus armeniacus</i> Focke	0.521	0.126
<i>Robinia hispida</i> L.	0.512	0.137
<i>Ampelopsis aconitifolia</i> Bunge	0.499	0.180
<i>Polygonum aubertii</i> Henry	0.499	0.180
<i>Wisteria sinensis</i> (Sims) DC.	0.469	0.177
<i>Parthenocissus tricuspidata</i> (Sieb. & Zucc) DC.	0.464	0.180

Table 4 Fit scores for individual species from the Bayesian model after cross-validation.

clear results. First, a small group of traits dominate the prediction of invasive potential in woody species in the New England region. Across all growth forms (shrubs, vines, and trees), plants with large native latitudinal ranges and rapid growth rates were

significantly more likely to have become invasive. Plants with evergreen leaves — the single most important trait — were by contrast significantly less likely to have become invasive (Table 2a,b). These results are consistent with previous studies

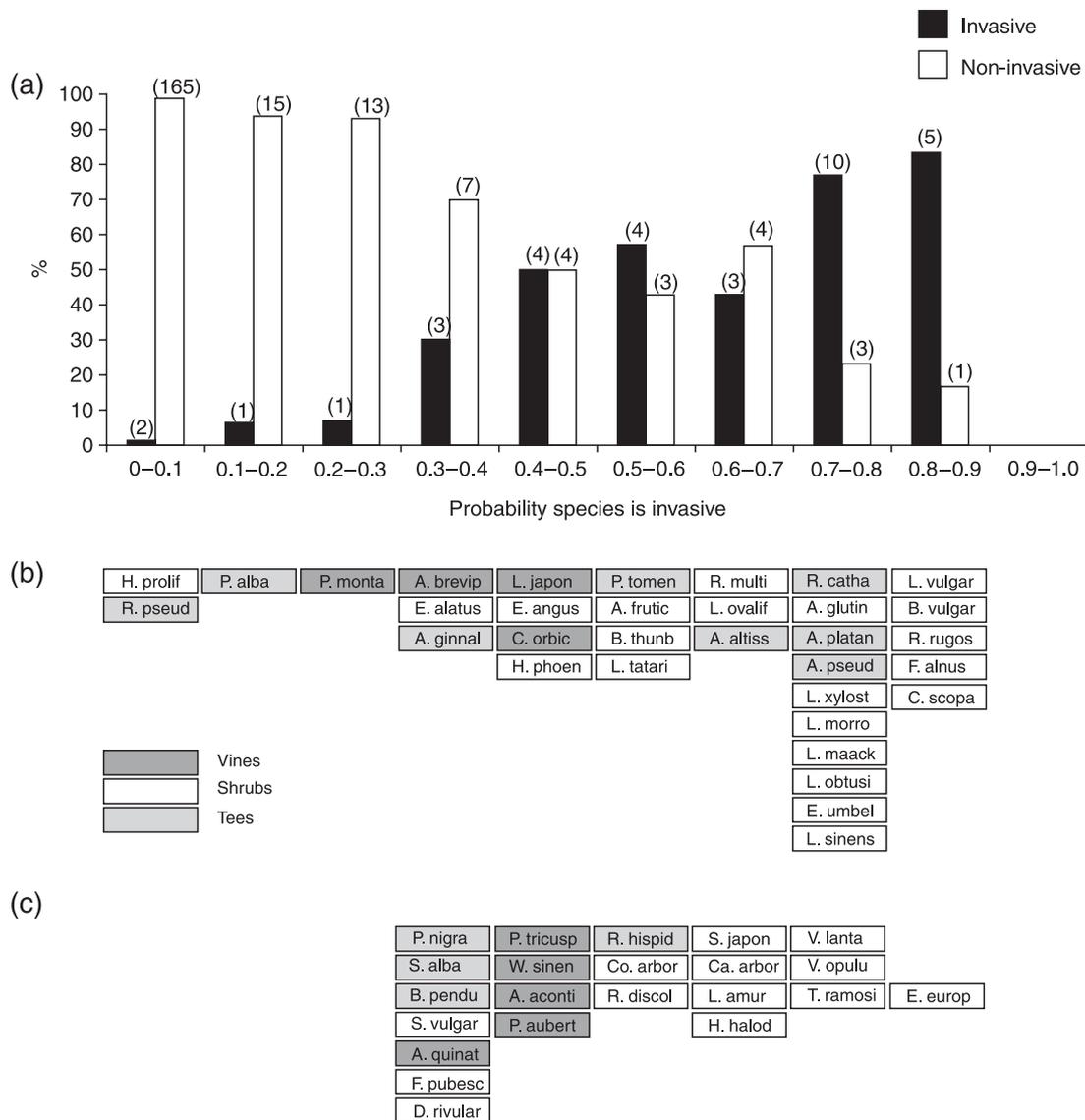


Figure 2 (a) Histogram of predictions for invasive and non-invasive species in Bayesian model with cross-validation. Bins along the x-axis represent the predicted probability of being invasive. Percentages along the y-axis represent the proportion of known invasive and non-invasive species in each bin (number of species in parentheses above each bar). (b) Location of currently recognized invasives in histogram. (c) Location of non-invasives with the highest predicted probability of being invasive. Refer to Table 3 and Appendix S1 for full names of all species

on woody plant invasiveness [large native range associated with invasiveness: Forcella & Wood, 1984; Rejmánek, 1995, 1996b, 1999; Williamson & Fitter, 1996; Goodwin *et al.*, 1999; high growth rate: Rejmánek & Richardson, 1996; Grotkopp *et al.*, 1998; Pattison *et al.*, 1998; Grotkopp *et al.*, 2002; evergreen plants being less invasive: Frappier & Eckert, 2003 (this study dealt with naturalization rather than invasiveness)]. The correlation between invasiveness and large native range of species may be associated with tolerance for wide environmental conditions and/or an indication of great dispersal ability (Booth *et al.*, 2003).

The analysis also revealed that even after trait differences are taken into account, species that become invasive in one region are significantly more likely to become invasive elsewhere (Table 2a). The application of previous invasion history as one of

the best predictors of future invasion is well supported in the literature (e.g. Forcella *et al.*, 1986; Daehler & Strong, 1993; Williamson & Fitter, 1996; Reichard & Hamilton, 1997; Horvitz *et al.*, 1998). The character 'invasive elsewhere' is not a life-history trait, however, and its strong predictive value suggests that beyond our set of plant characters, there are either additional traits that are difficult to measure, qualities special to each successful invasive, or unique circumstances (e.g. consistently high human dispersal rates, success in relatively generic human-disturbed conditions, as in the case of many agricultural weeds) that enable individual species to colonize successfully in multiple regions. As an example, the ability to escape particular types of diseases or pests may provide an important advantage for many invasives (Mack *et al.*, 2000; Mitchell & Power, 2003). In practical

terms, our findings further validate the use of the past global history of species in determining whether they are likely to pose a threat if newly introduced to any particular region.

Many previous studies that have used plant traits to try to predict invasiveness have derived a single suite of predictive characters across all of the species in the study (e.g. Reichard & Hamilton, 1997; Goodwin *et al.*, 1999). Yet part of the challenge of predicting invasiveness lies in the fact that there may be multiple successful strategies that allow species to succeed in their new environment. We hypothesized that different growth forms (trees, shrubs, and vines) would use different strategies or use different niches, and that these would be associated with different traits. To explore this possibility, we used a regression model that allowed the growth forms to vary in how their traits related to invasiveness. By using a hierarchical Bayesian model, instead of assuming complete independence among growth forms on the one hand, and identical response on the other, we allowed the data to inform how closely the growth forms covaried in their trait associations (Congdon, 2003). For most traits, including the dominant traits of evergreen-ness, growth rate, native range size, and invasive history, models showed that the traits bore the same relationship to invasiveness across all growth forms. This finding itself is useful, because it supports the emerging consensus across many studies that there is a small set of traits that appear to be strong universal predictors of plant invasiveness across regions, biomes, and plant growth forms.

There were, however, also identifiable differences among growth forms. Reproductive strategies presented the strongest contrast among growth forms, with different growth forms exploiting different modes of seed dispersal. For trees, wind dispersal is a relatively strong correlate of invasiveness (large positive coefficient, though not quite statistically significant; Table 2a), which implies that bird-dispersed trees in New England tend not to be invasive. By contrast, dispersal mode is only weakly correlated with invasiveness in both vines and shrubs. The lack of association between bird dispersal and invasiveness in shrubs is surprising, considering the role that birds play in dispersing some of the most visible invasives in New England (e.g. *Elaeagnus umbellata*), the fact that 18 of the 21 invasive shrub species listed by IPANE (Mehrhoff *et al.*, 2003) are dispersed by birds, and that having fleshy fruit is integral to the invasive spread of some species (e.g. *Frangula alnus*). However, the prevalence of bird dispersal and fleshy fruit as life-history traits in many 'non-invasive' shrubs in our data set means that 'bird dispersal' and 'fleshy fruit' are not good predictors of invasive potential. This provides a nice example of how invasive species need to solve multiple problems in order to establish widely and successfully: survival and vegetative spread alone are not sufficient, nor is efficient recruitment of dispersers.

The second character that emerges in contrast among the growth forms is shade tolerance. Invasive trees were more associated with shade tolerance than shrubs and vines. The model performance (DIC) was marginally improved by including the interaction term between growth form and shade tolerance. We expect this is true because the seeds of trees often are dispersed into closed canopy conditions and thus shade tolerance is

necessary for successful recruitment. For example, the invasive *Acer platanoides* is able to successfully penetrate even intact closed-canopy forests through its superior shade tolerance compared to that of other tree species (Webb *et al.*, 2000; Martin & Marks, 2006). In New England, due to the current regeneration of forests (Foster *et al.*, 1998), this shade tolerance is increasingly advantageous. Invasive shrubs often are successful in more secondary forest conditions, which have more open canopy conditions, while invasive vines are mostly edge species.

On the whole, vines were not classified effectively in the models with a large number of them yielding *P*-values close to 0.5 (Fig. 2). The poor discrimination of vines between invasives and non-invasives suggests two things about our vine data set. First, the small sample size of vines did not afford enough data for the model to discover correlations of trait combinations with invasive success. Second, it is possible that vines have very different traits associated with invasiveness than shrubs and trees, meaning that the models could not properly predict the invasive vines. Further research is needed to understand woody vines in light of the seemingly 'open niche' available to vines in North American temperate forests and the potential for many more liana introductions.

False positives

Our models identified 11 species as invasive (values of $P = \text{Prob}(\text{has become invasive}) > 0.5$) that are not currently listed as invasive in New England (i.e. 'false positives') (Table 4, Fig. 2). False positives can be viewed as a sign of weakness in our model because they represent species incorrectly predicted to be invasive when they are known to be in the landscape and non-invasive. But the information provided by these false positives is valuable as the basis for predicting what species may threaten New England habitats in the future, and/or reconsidering the basis of the decisions not to list them, since they represent a group of non-invasive species that share a group of traits with species invasive in New England. In many cases, the species that are false positives are currently widespread and naturalized — or even invasive — in other regions of North America. Included on this list are the shrubs, *Ca. arborescens*, *Colutea arborescens*, *E. europaeus*, *H. halodendron*, *L. amurense*, *Robinia hispida*, *Ru. armeniacus*, *S. japonica*, *V. lantana* and *V. opulus* var. *opulus*; as well as the tree *T. ramosissima*. Two recently introduced vines that had *P*-values < 0.5 also warrant attention as two species to watch: *P. aubertii* and *Am. aconitifolia*. The long lag-phase from introduction to invasion commonly seen in woody plants (Kowarik, 1995) may play a part in the classification of these species as 'false positives'. They simply may not have had sufficient time to become invasive.

False negatives

Our results include 11 false negatives (Table 4, Fig. 2) defined as species listed by IPANE as invasive in New England that are predicted by this model (some barely so) to be non-invasive. One of these missed species is the widespread invasive *E. alatus*,

suggesting that this species is different in some important way not captured by the suite of 28 included characters, and/or model assumptions. Examples of biological traits that might account for invasiveness of the species the model failed to classify correctly include the ability to fix nitrogen (i.e. *R. pseudoacacia*) and the tendency to leaf out very early in the spring and drop leaves late in the fall (i.e. *E. alatus*). Alternatively, there may have been differences in propagule pressure due to cultivation history, which ideally would be included in a model predicting invasion, but in practice are hard to quantify from historical data sources. In particular, the widespread popularity of the ornamental *E. alatus* has afforded it countless opportunities to introduce propagules into new habitats (Martine & Figley, 2007).

Finally, there may be species that are simply different from established invasives, but are using a novel successful invasion strategy. The inherent limitation of using a model that identifies invasive traits using the species already known to be invasive is exemplified by *Pyrus calleryana* (Callery pear). This commonly planted Asian tree has recently become an invasive threat in the eastern USA (Vincent, 2005). The species has fleshy fruits and bird-dispersed seeds (rather than wind-dispersed seeds, a significant correlate in invasive trees) and thus it is not selected by the model as a potential invader ($P = 0.047$).

Some of the species in the predictive Bayesian model incorrectly predicted to be non-invasive share the same deviations from typical invasiveness and these are addressed below. The most common atypical character shared by the false negatives is the possession of a relatively small native latitudinal range. Considering that large native latitudinal range arises as a significantly positive correlate with invasiveness, the fit scores of these species dip below 0.5 and the model misses them. The best examples of these are species with native ranges restricted by physical barriers (e.g. species endemic to the island nation of Japan). Of the eight species with the smallest native latitudinal range among the true (IPANE) invasives, four (*Ac. ginnala*, *Am. brevipedunculata*, *E. alatus*, and *R. pseudoacacia*) are also false negatives.

Prediction and management

We chose the value 0.5 to serve as a fair arbitrary value to place on measuring the strength of our models in discriminating between invasive and non-invasive plants. The Bayesian hierarchical mixed model that included the variable 'invasive elsewhere', and included recently introduced species successfully discriminated between invasive and non-invasive species 91% of the time after cross-validation. Because the model is relatively parsimonious and is based on a large data set, this high success rate does not result from 'overfitting' the particular species included in the data set.

This model focuses on learning about the traits and ecology of invasive plants in New England, but for comparative purposes the results from the cross-validated model should also be framed in terms of prediction as outlined by Smith *et al.* (1999). This discussion will focus solely on the cross-validated model of 165 plants introduced prior to 1900, since more recent introductions

could eventually turn out to be invasive. The sensitivity (proportion of known invasive species classified as invasive by the model) is 67% (22/33). The specificity of the model (proportion of non-invasive species classified correctly as non-invaders) is 93% (123/132). The positive predictive value (proportion of species classified as invasives that are true invasives), arguably the most important measure of the model's effectiveness (Pyšek *et al.*, 2004), is 71% (22/31). In terms of overall accuracy (proportion of all species assessed that were correctly categorized) our model yielded 88% (145/165), which compares favourably to previous models [78%: Perrins *et al.* (1992); 76%: Reichard & Hamilton (1997) (ignores coding errors, see Rejmánek *et al.* (2005); 66–85%: WRA in Australia and New Zealand Pheloung, 1995; see comments by Smith *et al.* (1999), and 86%: Kõivánek & Pyšek (2006)]. Our model contrasts with the above models by having lower sensitivity than most of these models, but higher specificity [93% vs. e.g. 71%; Reichard & Hamilton (1997)].

Smith *et al.* (1999) have shown that despite the relatively high accuracy of previous predictive models, if we assume a realistically low base rate of plant invasiveness, these models would erroneously bar many more non-invasive species than invasive ones. Thus in practice, the costs of using such screening methods in terms of restricting valuable imported species (false positives) could easily outweigh the benefits of successfully barring entry of invasive species (Pyšek *et al.*, 2004). Our model performs relatively well from this perspective because of its high specificity rate. For example, if we assume a base invasiveness rate of 2% (lower than the 14% prevalence of invasives in our data set, which is almost certainly an overestimate) (see Smith *et al.*, 1999), it would be rational to use this model to screen introductions if allowing an invasive into the region imposes costs greater than about five times those of barring a useful non-invasive (prediction likelihood ratio of $LR = (22/33)/(9/132) = 9.8$, vs. a threshold of $LR_{\min} = 1/(0.02 \cdot 5) = 10$ (Smith *et al.*, 1999).

While we are not attempting to justify using this particular model for screening, our results are encouraging. The specificity of the model would be further improved if we incorporated some of the species introduced more recently than 1900 (none of which is currently classified as an invasive). Furthermore, most of these species were introduced for the horticulture trade rather than for agriculture (Reichard & White, 2001), and there is likely a great deal of substitution that can be made among plants to reduce costs of restricting plants (Kõivánek & Pyšek, 2006). Finally, models like this can be used in a more flexible way to generate multiple classification categories – e.g. admit if $P < 0.3$, do not admit if $P > 0.5$, and further analysis needed if $0.3 < P < 0.5$ as suggested in Reichard & Hamilton (1997) – further reducing this cost of screening (see Table 5).

The predictive framework outlined in this paper supports the consensus that certain plant traits (e.g. fast growth rate) are frequently associated with the ability of woody plants to invade new habitat. Contrasting results among the growth forms in dispersal strategy and shade tolerance demonstrate that there are a number of different trait combinations that allow successful invasion in the same geographical area. The combinations of traits that emerged at the level of growth form in our analysis

Table 5 Possible classification and management scheme that emerges from segregating probability of invasiveness into three groups.

P	Invasive		Non-invasive		Management
	N	%	N	%	
0.5–0.9	22	(66%)	11	(5.1%)	Reject
0.3–0.5	7	(21%)	12	(5.6%)	Hold
0–0.3	4	(12%)	193	(90%)	Accept

point to a variety of niches available for invasion even in a relatively narrowly defined region. Including growth form in our model added predictive strength as it allowed for these multiple invasive strategies to emerge. Furthermore, the models identified a number of potential problem species for which current and future monitoring are warranted (Martine *et al.*, in prep.). Some of these ‘false positives’ (e.g. *P. aubertii*) are already on the ‘radar screens’ of local botanists as possible emerging threats. The identification of already introduced plants as potentially invasive species is an important part of a screening or monitoring programme (Richardson & Pyšek, 2006). Finally, models employed in invasive plant prediction, though they can be effective and attractive methods represent but one element in the biologist’s toolbox. Field observation, growth trials, and experimental research are each still indispensable in understanding the invasive potential of introduced plant species.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Data set of all measured traits for 248 woody species introduced into New England. Includes description of coding for all characters.

Appendix S2 Model coding for Bayesian logistic regressions implemented in OPENBUGS.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1472-4642.2007.00381.x>
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