Pine invasions: climate predicts invasion success; something else predicts failure

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\textbf{INTRODUCTION}

Predicting where a species will invade and, equally importantly, where it will not invade is an important challenge for invasion ecology. Many hypotheses have been proposed to explain the success and failure of exotic species. Some of them relate to abiotic factors, such as climate matching (Williamson, 1996; Curnutt, 2000; Thuiller \textit{et al.}, 2005; Richardson & Thuiller, 2007). Propagule pressure is also widely acknowledged as a crucial factor in invasions (Lockwood \textit{et al.}, 2005). Several studies have focused on how different factors affect invasions (Bucharova & Van Kleunen, 2009; Pyšek \textit{et al.}, 2009; Carrillo-Gavilan & Vila, 2010; Essl \textit{et al.}, 2010), but much recent work predicting the geography of invasions has focused on the characteristics of the abiotic environment, especially as a predictive tool.

Climate-based species distribution models have been increasingly used to predict invasions because data to build the models are widely available and they have generally proven accurate for modelling native species distributions (Peterson, 2003; Zhu \textit{et al.}, 2007; Phillips & Dudík, 2008). These models predict species distributions based on occurrence data and detailed environmental and/or climatic data sets (Peterson & Holt, 2003). There is strong evidence that climate plays an important role explaining species distributions (Gaston, 2003),

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\textbf{ABSTRACT}

\textbf{Aim} Explaining why some invasions fail while others succeed is a prevailing question in invasion biology. Different factors have been proposed to explain the success or failure of exotics. Evidence suggests that climate similarities may be crucial. We tested this using 12 species of the genus \textit{Pinus} that have been widely planted and shown to be highly invasive. \textit{Pinus} is among the best-studied group of exotic species and one that has been widely introduced world-wide, so we were able to obtain data on invasive and non-invasive introductions (i.e. unsuccessful invasions; areas where after many decades of self-sowing seeds there is no invasion).

\textbf{Location} World-wide.

\textbf{Methods} We developed species distribution models for native ranges using a maximum entropy algorithm and projected them across the globe. We tested whether climate-based models were able to predict both invasive and non-invasive introductions.

\textbf{Results} Appropriate climatic conditions seem to be required for these long-lived species to invade because climates accurately predicted invasions. However, climate matching is necessary, but not sufficient to predict the fate of an introduction because most non-invasive introductions were predicted to have triggered an invasion.

\textbf{Main conclusions} Other factors, possibly including biotic components, may be the key to explaining why some introductions do not become invasions, because many areas where \textit{Pinus} is not invading were predicted to be suitable for invasion based solely on climate.

\textbf{Keywords} Biological invasions, biotic resistance, climate matching, forestry, Pinaceae, \textit{Pinus}.

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© 2011 Blackwell Publishing Ltd

DOI: 10.1111/j.1472-4642.2011.00772.x

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including invasives, because temperature and other climatic variables have a deterministic relationship with species distributional area (Pulliam, 2000; Soberón & Nakamura, 2009). However, climate-based models generally ignore other variables (e.g. biotic interactions) shown through rigorous empirical ecology to affect species invasions (e.g. Richardson et al., 2000a; Maron & Vilá, 2001; Mitchell et al., 2006). Many studies have shown that models are rather accurate for predicting sites of introduction, but their ability to predict spread in introduced areas is inconsistent (Broennimann et al., 2007; Fitzpatrick et al., 2007; Rödder et al., 2009; Medley, 2010). Furthermore, few studies are conducted on non-invasive introductions, i.e. cases where species have failed to become invasive despite high introduction efforts and long residence times. Such studies can provide vital information on invasion mechanisms (Diez et al., 2009) and may provide tools for the management of exotic species. Because of our lack of understanding of these failed invasions, we run the risk of falsely predicting an invasion where one might not occur. A key question that remains is: How accurate are climate-based models at predicting failed invasions? In this paper, we use species distribution models to test the ability of climate alone to determine invasiveness of Pinus species in non-native regions.

The genus Pinus is probably the best-studied group of invasive plants and has been suggested as a model group to understand plant invasions (Richardson, 2006). Pinus species have been widely planted, and their ecology and use as forestry species have been studied in both their native and introduced ranges (Richardson, 1998a,b). There are many studies on various aspects of their invasion, and the Pinus genus has ample records of successful invasions (Richardson et al., 1994; Rejmánek & Richardson, 1996; Richardson & Higgins, 1998; Buckley et al., 2005). Also, unlike most invasive species, it also has ample records on non-invasive introductions (Simberloff et al., 2002; Adamowski, 2004; Bustamante & Simonetti, 2005; Mortenson & Mack, 2006). Of the 111 species in the genus, 22 are known to be invasive in at least one region (Richardson & Rejmánek, in press). Given known traits of Pinus species, it is possible to predict the intrinsic invasiveness of each species based on discriminant functions developed by Rejmánek & Richardson (1996; see also Richardson & Rejmánek, 2004). Therefore, the goal of this research is to determine how well climate-based models can predict whether an introduction will become an invasion (Richardson et al., 2000b) for invasive members of the Pinus genus. If models match invasiveness (i.e. predict high-risk areas where the species is invasive, and low to no risk where it has not become invasive but is present in a forestry plantation with thousands of reproductive trees), then climate is highly important to invasibility. Alternatively, if climatic models predict successful invasions, but also predict high-risk areas where invasions do not occur despite the presence of an introduced population, other variables are also responsible for determining invasibility. We expect that models using climate will be better at predicting successful invasions, but will over-predict the geography of non-invasive introductions. Our reasoning is that climate matching has proven successful for deciding locations for plantations, but it is known that biotic interactions and other factors not directly related to climate are important for silviculture (e.g. pest avoidance) and for the global invasion of this genus (Rouget & Richardson, 2003; Richardson & Rejmánek, 2004; Bustamante & Simonetti, 2005; Nuñez et al., 2008a). Non-invasive introductions (failed introductions), then, may be more difficult to predict based on climate, as they may be a response to idiosyncratic factors such as biotic interactions including effects of parasites or competition with local plant species.

**METHODS**

**Study species and distribution data**

To evaluate the role of climate for Pinus invasions, we developed species distribution models for 12 Pinus species in their native range and determined whether the models were able to predict pine invasions in areas where they are not native (different biogeographical region) (see Table 1). We created models for P. banksiana, P. contorta, P. elliottii, P. halepensis, P. muricata, P. nigra, P. patula, P. pinaster, P. ponderosa, P. radiata, P. strobus and P. sylvestris using occurrence data from native ranges obtained from the Global Biological Information Facility (http://www.gbif.org), the US Department of Agriculture (http://www.plants.usda.gov), and by surveying the literature (Godbout et al., 2005; Zha et al., 2009). Pine occurrences in non-native regions represented either (1) points where pine plantations were located and the species had not invaded the surrounding landscape or (2) points where the species had become invasive in the non-native region (see ‘Defining invasions’ for details). We selected these 12 Pinus species for several reasons. First, these species possess a combination of life history traits that have shown to confer high probabilities of invasion and are known to be highly invasive in different regions of the world (Rejmánek & Richardson, 1996; Richardson & Rejmánek, 2004). These species have been widely planted outside their native range and have been recorded to invade on at least two continents (Rejmánek & Richardson, 1996; Richardson & Rejmánek, in press). Further, these are the same 12 highly studied species of invasive pines that Rejmánek & Richardson (1996) used to develop a discriminant function to predict pine species invasion. Finally, and perhaps most importantly for the current study, for most of these species, there are also recorded locations where the pines failed to invade despite persistence in silvicultural plantations. Thus, data are available from invaded and non-invaded areas, unlike for most introduced species.

**Model development**

We generated species distribution models using a maximum entropy algorithm implemented in MAXENT software v3.3.2 (Phillips et al., 2004, 2006). Maximum entropy is a machine-learning technique that predicts species distributions using
Table 1 List of the studied species, their native region, intrinsic invasiveness (following Rejmánek & Richardson (1996); species with positive Z-scores are expected to be invasive) and locations where they have been recorded as invasive or non-invasive. For more detail on the locations used in our models, see Appendix S1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Native region</th>
<th>Intrinsic invasiveness (Z-score)</th>
<th>Locations of recorded invasions</th>
<th>Locations of recorded non-invasive introductions</th>
<th>References</th>
</tr>
</thead>
</table>
detailed climatic and environmental data sets together with species occurrence data and generally performs better than other algorithms in tests of model performance (Elith et al., 2006; Phillips et al., 2006; Ortega-Huerta & Peterson, 2008). Maximum entropy uses presence-only data sets to predict the suitability of habitat and is quite robust to spatial errors in occurrence data (Phillips et al., 2006; Graham et al., 2008).

Some species have large occurrence data sets (up to 59,080 points for *P. sylvestris*) that vary in spatial density based upon sampling intensity and geography. Therefore, we selected points for model development using a subsampling regime we developed that (1) reduced sampling bias across countries/ political boundaries and (2) eliminated spatial autocorrelation of model residuals, a problem for distribution modelling algorithms recently discussed in the literature (Dormann et al., 2007; Veolo, 2009). First, we generated models using all available occurrence points and measured spatial autocorrelation among model pseudo-residuals (1 – probability of occurrence generated by model) by calculating Moran’s *I* at a grid whose cell dimensions were the distance at which spatial autocorrelation ceased and randomly selected one occurrence point in each grid cell. Minimum distances (grid dimensions) differed by species and ranged 75–583 km depending on the degree of spatial autocorrelation detected. This procedure substantially reduced the number of occurrence points used in models (from upwards of 59,000 to < 100 points) and eliminated spatial autocorrelation. Moreover, this technique eliminated sampling bias and resulted in evenly distributed occurrence points across political boundaries.

We included six 2.5 arc-minute environmental data sets in our models based upon their importance to *Pinus* ecology. Five were obtained from the WORLDCLIM database (Hijmans et al., 2005): annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the wettest month and precipitation of the driest month. Nineteen variables are available from the WORLDCLIM database, but because some are highly correlated with one another, we chose variables representing mean values and extremes (because many taxa are limited by environmental extremes). We also included mean number of frost days from the CRU CL 2.0 database (New et al., 2002). Model generation was confined to the native range and then projected across the globe.

**Model testing**

Prior to global projection, model accuracy for native ranges was evaluated in two ways. For model generation, we used occurrence points with an enforced distance from one another (described above) and used the remainder of the points not used in model generation to test each model using binary tests of omission (Phillips et al., 2006). We calculated omission rates as the proportion of test points that were not predicted at a threshold probability that equaled the minimum probability of any pixel containing an occurrence point. Secondly, we evaluated model accuracy using the area under the curve (AUC) of the receiver operating characteristic (ROC) plot. AUC is a composite measure of model performance. AUC values range from 0 to 1, where 1 is a perfect fit. Useful models produce AUC values of 0.7–0.9, and models with ‘good discriminating ability’ produce AUC values above 0.9 (Swets, 1988).

**Predictive ability for invasions**

**Defining invasions**

To evaluate the ability of models to predict invasions, we obtained non-native occurrences from the Agricultural Georeferenced Information System of South Africa (AGIS), from personal observations of local experts (Nicholas Ledgard for New Zealand, Rafael Zenni for southern Brazil, Moira Williams for south-eastern Australia, M. Amparo Carrillo-Gavilán for Europe, Martin Krivanek for the Czech Republic and Barbara Langdon from Chile) and from the literature, and we coded each occurrence as either ‘invasive’ or ‘non-invasive’. Some articles provided specific points or maps from which we could obtain geographical coordinates. Other references provided only a vague verbal description of where an invasion was located, for example ‘In North-eastern Victoria, Australia, *P. nigra* has invaded natural eucalyptus forests’ (Richardson et al., 1994). Such descriptions did not allow us to collect geographical coordinates, so we were unable to use those points. To determine that an invasion was successful (‘invasive’), the species needed to be abundant and regenerating outside the original plantations and needed to be producing reproductive offspring at a distance further than 100 m from the plantation (see, Richardson et al., 2000b). For non-invasive introductions (‘not invasive’), the species needed to be absent or very rare outside the original plantations after a period of time long enough that it could have spread (not < 40 years; note that most of these species reach maturity before they are 10 years old) and in areas where a large number of individuals were planted (e.g. commercial plantations). Also, all the records of non-invasive introductions were based on indications that the researchers studying the sites found them anomalous enough to notice an absence of invasion as important enough to record. Because of the time lag phenomenon (Crooks & Soule, 1999; Pyšek et al., 2009), we recognize that defining non-invasion events is problematic (see discussion in Rejmánek et al., 2005). However, we suggest that it is clear that in these areas, something has thus far prevented the invasion because seeds have been available from parental trees for decades without noticeable establishment having taken place.

**Evaluating models**

To evaluate the ability of native models to predict invasion vs. non-invasion, we projected each model across the globe and...
placed non-native occurrence points onto generated distributions in a GIS (ArcGIS; Environmental Systems Research Institute, Redlands, CA, USA). To balance the number of non-native points between regions for statistical comparisons, we randomly selected one occurrence point from each non-native range (i.e. continent where the species is not native) for each invasion category (i.e. invasive, non-invasive). By doing this, we eliminated the possibility of introducing bias towards species that had multiple occurrence points in one region per invasion category. We recognize that this substantially reduces the number of points available for our statistical analysis, but reducing sampling bias in this way primarily reduces the number of invasive points without affecting the number of non-invasive points related to each introduction event. Because the number of invasive points is, by default, greater than the number of non-invasive points simply because invasions spread from points of introduction, we reduced invasion status bias this way. We categorized non-native occurrences as ‘predicted’ or ‘not predicted’ based upon the probability of occurrence for each occurrence point. Points were ‘predicted’ if the probability was equal to or greater than the minimum threshold probability for each native model (minimum probability for any occurrence point using for model training, Liu et al., 2005). We pooled data (predicted vs. not predicted) for all non-native points across species to perform the statistical tests. Currently, there is not enough information at the studied scale, especially on failed invasions, to perform calculations for individual species, but all these highly invasive Pinus species share numerous traits. To evaluate the ability of climate-based distribution models to predict species invasions vs. no invasion in non-native areas, we constructed a 2 × 2 contingency table with the following categories: predicted, not predicted, invasive and not invasive. We used Fisher’s exact test to test the null hypothesis that invasion status of non-native occurrences (invasive, non-invasive) was not associated with model prediction (predicted, not predicted). If the abiotic environment (as included in our models) is the limiting factor determining invasion status, then we expect a significant association between invasion status and model prediction. Alternatively, if some other factor such as biotic conditions determine invasion status, there will be no significant association between invasion status and model prediction (i.e. models will predict all non-native occurrences, independently of invasion status at a 2.5 arc-minute grid size).

**RESULTS**

Models for each of the 12 Pinus species (Appendix S1) provided a good fit and consistent predictability for native test points (Table 2). AUC values for 11 of the 12 native models exceeded 0.90, indicating ‘good discriminating ability’ (Table 2). The AUC for P. patula was slightly lower (0.89), but this value still indicates a good fit and a useful model (Table 2). Threshold-dependent omission rates for test points ranged 0–3% for 11 species, and 14% (out of 494 points) for P. ponderosa (Table 2). Random selection of non-native occurrence points in each region by invasion status yielded 48 points (of originally 160) with which to evaluate model prediction (Table 1). We ran these analyses several times with different random points and conclusions did not change, suggesting that this method avoided over-representing one invaded or non-invaded region relative to others. Analyses of independence revealed that invasion status for non-native points was independent of model prediction (Table 3, Fisher exact test, \( P = 0.42 \)). Specifically, for 25 points representing invasive populations, models accurately predicted 20 and failed to predict 5 points. For the 23 non-invasive points, models were mostly inaccurate: models predicted high-risk areas where the species were not invasive for 21 points and predicted a low

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**Table 2** Model output characteristics for 12 Pinus species. \( N \) represents the number of occurrence points used for model training and testing. AUC (area under the curve of the receiver operating characteristic) is a composite measure of model performance. AUC values range from 0 to 1, where 1 is a perfect fit. Useful models produce AUC values of 0.7–0.9, and models with ‘good discriminating ability’ produce AUC values above 0.9 (Swets, 1988). Min. train. represents the minimum probability of occurrence assigned to occurrence points used for model training. Test omission is a threshold-dependent value of model performance indicating the percent of test points not predicted at a given threshold. The threshold here is defined as the Min. train. value. Lower values indicate better predictive ability for test points.

<table>
<thead>
<tr>
<th>Pinus species</th>
<th>( N ) (train, test)</th>
<th>AUC (train)</th>
<th>AUC (test)</th>
<th>Min. train.</th>
<th>Test omission (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. banksiana</td>
<td>30, 175</td>
<td>0.89</td>
<td>0.91</td>
<td>0.21</td>
<td>1.0</td>
</tr>
<tr>
<td>P. contorta</td>
<td>23, 269</td>
<td>0.91</td>
<td>0.93</td>
<td>0.20</td>
<td>3.0</td>
</tr>
<tr>
<td>P. elliottii</td>
<td>26, 139</td>
<td>0.97</td>
<td>0.97</td>
<td>0.21</td>
<td>0.0</td>
</tr>
<tr>
<td>P. halepensis</td>
<td>66, 265</td>
<td>0.93</td>
<td>0.97</td>
<td>0.04</td>
<td>0.0</td>
</tr>
<tr>
<td>P. muricata</td>
<td>13, 79</td>
<td>0.93</td>
<td>0.97</td>
<td>0.14</td>
<td>0.0</td>
</tr>
<tr>
<td>P. nigra</td>
<td>27, 1000</td>
<td>0.92</td>
<td>0.95</td>
<td>0.06</td>
<td>0.9</td>
</tr>
<tr>
<td>P. patula</td>
<td>9, 25</td>
<td>0.90</td>
<td>0.89</td>
<td>0.21</td>
<td>0.0</td>
</tr>
<tr>
<td>P. pinaster</td>
<td>17, 3679</td>
<td>0.92</td>
<td>0.95</td>
<td>0.03</td>
<td>0.0</td>
</tr>
<tr>
<td>P. ponderosa</td>
<td>22, 494</td>
<td>0.97</td>
<td>0.95</td>
<td>0.29</td>
<td>14.0</td>
</tr>
<tr>
<td>P. radiata</td>
<td>14, 1</td>
<td>0.97</td>
<td>0.93</td>
<td>0.24</td>
<td>0.0</td>
</tr>
<tr>
<td>P. strobus</td>
<td>26, 605</td>
<td>0.93</td>
<td>0.95</td>
<td>0.10</td>
<td>0.0</td>
</tr>
<tr>
<td>P. sylvestris</td>
<td>42, 1430</td>
<td>0.93</td>
<td>0.94</td>
<td>0.23</td>
<td>0.9</td>
</tr>
</tbody>
</table>
probability of occurrence for two non-invasive points, so only two points of 23 were accurately predicted (Table 3). Thus, models positively predict non-native occurrences regardless of whether they are invasive. See supplementary information for the maps for all the 12 species. We provide mapped data for *Pinus ponderosa* as a visual example (Fig. 1).

**DISCUSSION**

These results show that climate-based distribution models can predict areas at risk of invasion, but that the transition from introduced to invasive is clearly also regulated by factors other than climate. Climate may be a key factor explaining the minimum requirements for the species to thrive, but having a similar climate with the native region may not suffice to ensure success. For instance, biotic interactions that are novel or that differ in intensity from the native range can prevent a species from establishing and spreading in a non-native area (Richardson *et al.*, 2000a; Maron & Vila, 2001; Mitchell *et al.*, 2006; Nuñez *et al.*, 2008b, 2009). The inability of climate-based models to predict lack of invasiveness of *Pinus* can likely be explained by biotic interactions. Factors such as seed predation, mycorrhizal facilitation, competition with local plants and herbivory can have strong effects on *Pinus* establishment and survival. Pine species have been shown to be severely affected by biotic interactions in both their native range (Castro *et al.*, 2002; Rogers *et al.*, 2006; Richardson *et al.*, 2007; Brodribb & Feild, 2008; Collier & Bidartondo, 2009) and their exotic range (Becerra & Bustamante, 2008; Nuñez *et al.*, 2008b, 2009). Therefore, it is likely that the absence of invasion after introduction and sufficient residence time may be attributed to biotic factors (Simberloff *et al.*, 2002).

Incongruence between model predictions and invasions may be partly because exotic species may not yet be in equilibrium with their new environment (Simberloff *et al.*, 2010). For instance, Montoya *et al.* (2009) found that spatial clustering of invasive tree patches was more intense (i.e. more clustered) than predicted by distribution models. Models may predict smooth gradients of abundance and invasions may follow such trends initially, whereas over time biotic interactions may enforce increased spatial structure. Our analysis was at a scale where this may not be a problem. All non-native occurrence points were in areas where the exotics are successfully invading...

**Table 3** Contingency table for non-native *Pinus* occurrence data showing instances where niche-based models predicted (or not) invasive and non-invasive *Pinus* locations in non-native regions. Fisher’s exact test revealed invasion status, and model prediction was independent (*P* = 0.42), and models predict high-risk areas even where *Pinus* were present but not invasive. ‘Predicted by model’ means that models predicted areas where pines are highly likely to occur. For instance, for 23 instances where a *Pinus* species was present in a plantation but did not become invasive (Invasive: No), models predicted high risk 21 times and indicated low-risk (accurately) twice.

<table>
<thead>
<tr>
<th>Invasive</th>
<th>Predicted by model</th>
<th>Total</th>
<th>Pr (invasive)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
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</tbody>
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<table>
<thead>
<tr>
<th></th>
<th>Yes</th>
<th>No</th>
<th>Total</th>
<th>Pr (predicted)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td>21</td>
<td>2</td>
<td>23</td>
<td>0.48</td>
</tr>
<tr>
<td>Yes</td>
<td>20</td>
<td>5</td>
<td>25</td>
<td>0.52</td>
</tr>
<tr>
<td>Total</td>
<td>41</td>
<td>7</td>
<td>48</td>
<td></td>
</tr>
</tbody>
</table>

\(Pr (predicted) = 0.85, 0.15\)

**Figure 1** Maxent model for *Pinus ponderosa* for its native range (a) and projected onto South America (b) and Australia (c). Open circles represent native occurrences used to train the model, and stars show locations used in tests of independence. The native model predicted one invasive occurrence in Chile (b), but failed to predict an invasion in Australia (c), although the model predicted a region adjacent to the invasion.
(so there are no major limiting factors), or when they failed, we obtained points from areas adjacent to the plantations (at just metres from them), and where the species were allowed enough time to colonize (40+ years total, and all these species start seed production before c. year 10). Thus, even when species may not be in equilibrium with the environment, they had enough time to colonize the studied areas. Climatic niche shifts can occur during invasion as a result of, e.g., realized niche differences or adaptation to new conditions, causing discrepancies between predicted and actual areas of invasion (Broennimann et al., 2007; Fitzpatrick et al., 2007). Shifts in the realized niche in non-native regions can occur through biotic interactions (above) or dispersal barriers in the new region that prevent the species from occupying all areas that satisfy its fundamental niche requirements. Because the Pinus species that we considered are primarily wind dispersed, dispersal limitation is probably not a major issue. Also, given the relatively long generation time of pines, the possibility for adaptation is less than that of some other species (e.g. annual plants), owing to the reduced opportunity to evolve in short time periods (c. from 35 to 100 years). Moreover, selective pressure may be diminished because climate in the area of introduction is similar to that of native regions for the species we evaluated.

Propagule pressure may be playing a role in our results (Richardson et al., 1994; Rouget & Richardson, 2003). If in some areas few trees or plantations have established, it is likely that they will have fewer chances of invasion (Pyšek et al., 2009). However, all of our study sites were associated with forestry plantations where thousands of trees were planted and grew successfully. Simberloff et al. (2010) found that introductions of small populations of exotic conifers (e.g. for ornamental use) rarely trigger invasion, but that forestry practices have the potential to start pine invasions by increasing propagule pressure. Indeed, Essl et al. (2010) corroborated these results for Pinaceae. Therefore, we suspect that because our studied sites contain many individuals of introduced trees and we studied areas adjacent to the plantations, propagule pressure probably plays a relatively minor role in explaining our results. Also, it has been proposed that for Pinaceae, other factors may be more important than propagule pressure to explain their invasion (Rejmánek et al., 2005; Nuñez et al., in press).

Our results for Pinus highlight the potential importance of both biotic interactions and climate for predicting invasions. Such factors may be even more essential to predict invasions for other species. Most Pinus species (and all the ones included in this study) are largely wind dispersed and do not depend on animal vectors for seed dispersal, and all are wind pollinated; this makes them less dependent on other species for their success than is the case with many invasive plants. They do rely heavily on specialized ectomycorrhizal fungi for their establishment and growth, which can be a limitation for their invasion (Nuñez et al., 2009). However, they do not rely heavily on mutualisms for other aspects of their life cycle. These characteristics together could make them less susceptible to biotic effects than many other plants that depend on other species for some basic aspects of their life cycle. For example, invasions of Ficus species have been triggered in some cases by the arrival of very specific pollinators that are essential for reproduction (Richardson et al., 2000a). Therefore, it is possible that for other species, biotic factors may be even more important than for the 12 Pinus species that we studied. Thus, climate-based models might be even less accurate for predicting non-invasive introductions in other species that heavily rely on different biotic interactions, such as mutualisms. Nevertheless, biotic interactions are likely to be playing a key role on our results, producing the observed errors in the predictions.

The incongruence between model predictions and invasion success supports recent work that reveals the inadequacy of the native environment in predicting the extent of invasions. Recent studies have shown that commonly used modelling approaches may underestimate the importance of mechanisms facilitating biological invasions (Kearney et al., 2008). Thus, many researchers are calling for more sophisticated models that include, for example, aspects of the physiology of the species and spatial habitat structure in non-native regions (Kearney & Porter, 2009). While developing more realistic models that incorporate more species biology and ecology is necessary to predict invasive species spread more accurately (Gallien et al., 2010), simple climatic models are useful for testing hypotheses relating climate to some aspects of the process of biological invasions. Moreover, climatic models have proved quite effective for predicting introduction sites for species that subsequently become invasive and so could provide a means for focussing eradication efforts during the early stages of invasion (Broennimann et al., 2007; Fitzpatrick et al., 2007; Medley, 2010).

In conclusion, this study highlights the importance of the multiple factors that are required for an invasion to succeed. This study also emphasizes the importance of studying failed invasions as well as successful ones (Diez et al., 2009), because limiting our results to successful invasions would have resulted in very different interpretations.

ACKNOWLEDGEMENTS

We thank B. Van Wilgen, N. Ledgard, M. Williams, R. Zenni, M. Amparo Carrillo-Gavilán, Martin Krivanek, and Petr Pyšek for very generously sharing their data and M. Fitzpatrick for helpful comments and help and encouragement in early stages of this project. D.M. Richardson provided detailed editorial comments that greatly improved the manuscript. We also thank W. Godsoe, H. Kalkvik, R. Dimarco and D. Simberloff for helpful comments. Funding was provided by NSF (DEB 0948930).

REFERENCES


**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Maxent models for each of 12 *Pinus* species. Model calibration was restricted to native regions and projected across the globe. Small open circles represent points used to train models, and filled circles show occurrences in non-native regions. Stars indicate points used in tests of independence.

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**BIOSKETCHES**

Martin A. Nuñez has a broad interest in biological invasions. He has studied factors that promote or deter the establishment and expansion of exotics. His main research interest includes the factors governing pine invasion, how multiple factors interact to explain species establishment, and the role of soil biota in plant invasion. Other research interests include conservation of Patagonian ecosystems, biogeography, and dispersal ecology.
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Author contributions: M.A.N. and K.A.M. conceived the ideas; M.A.N. and K.A.M. collected the data; M.A.N. and K.A.M. analysed the data; and M.A.N. and K.A.M. led the writing.

Editor: David Richardson