Predicting successful replacement of forest invaders by native species using species distribution models: The case of Pittosporum undulatum and Morella faya in the Azores

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Abstract

Invasive alien species have taken the place of native forest species worldwide, and particularly in island systems like the Azores. Species distribution models could be used to support the design of control strategies, including the definition of target areas. In this study we used species distribution modelling, performed with the ecological-niche factor analysis (ENFA) approach. Pittosporum undulatum is the most widespread woody invader in the Azores where it is considered as one of the priority species for control actions. On the other hand, Morella faya is a native woody plant facing several threats, including plant invasions. This paper aims to evaluate whether and where areas currently occupied by P. undulatum could also be favorable habitat for M. faya, thus providing support for future management actions. Occurrence data on P. undulatum and M. faya from a forest inventory were randomly split into training and testing datasets. Twenty six ecogeographical variables were used together with the training datasets in modelling. The modelling results were validated based on the continuous Boyce curve calculated with the testing datasets. We selected and compared the models of the highest predictive power and robustness for both species to define where M. faya could inhabit areas currently occupied by P. undulatum. The two species have quite similar environmental preferences, which correspond mainly to coastal lowlands and forested habitats characterized by relatively high temperature and wide ranges of low relative humidity values. The main difference between both species is that M. faya was considered more specialized according to current data. M. faya could potentially be used to replace P. undulatum in up to 24% of the Azorean area currently invaded, mostly in São Jorge and Pico Islands. According to our results, the ENFA modelling approach revealed to be a useful tool in the design of more efficient management strategies for woody plant invaders.

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1. Introduction

Native plant communities are often disturbed by alien species (Denslow et al., 2009; Fornwalt et al., 2003; Keane and Crawley, 2002; Lake and Leishman, 2004; Pyšek et al., 2002). Globally, alien species can produce dramatic changes in the ecosystems affecting biodiversity, forestry, farming, hydrologic cycles and human health, especially in islands due to their vulnerability and to the peculiarities of the native island biota (Caupé-Castells et al., 2010; Olesen et al., 2002; Ramos, 1996; Silva et al., 2008; Simberloff, 1995).

In the Azores archipelago, invasive alien species are an important threat to biodiversity conservation (Castro et al., 2010; Kueffer et al., 2010; Silva et al., 2008; Silva and Smith, 2004, 2006), which is emphasized by the fact that the Azores is included within the Macaronesian region, which is part of the Mediterranean biodiversity hotspot (Myers et al., 2000). No less than 60% of the...
approximately 900 species of vascular plants inhabiting the Azorean islands were introduced by human activities, and are now considered as either naturalized or frequently escaped (Silva et al., 2010; Silva and Smith, 2004, 2006).

The most important woody invasive species, Pittosporum undulatum Vent. (Pittosporaceae), is a shrub or tree up to 15 m tall, native from Australia. Several actions to replace P. undulatum by Macaronesian species are taking place within the framework of government initiatives and LIFE projects. One of the native species considered in those projects is Morella faya (Aiton) Wilbur (Myricaceae). Present in the entire archipelago, with a wider distribution in the past, and without the limitations imposed by the use of endemic species (e.g. the conservation of particular genetic traits present in specific populations), it is a good candidate to replace P. undulatum (Droué, 1866; Sjögren, 1973; Silva et al., 2011). However, the choice on what and where to plant is guided by common sense. Thus, a knowledge base for sound decisions would be of great relevance.

To find ecologically suitable places for M. faya where P. undulatum is currently invading, the records of both species in a forest inventory were used for modelling. Modelling is a popular approach to predict species distributions, that have been used to evaluate the potential distribution of invasive plant species (e.g. Crossman et al., 2011; Hortal et al., 2010; Kleinbauer et al., 2010; Mgidi et al., 2007; Trehowan et al., 2011) and to support the design of control strategies, including the definition of target areas (e.g. Mukherjeea et al., 2011). Thus, although species distribution models have been used to model invaders, including P. undulatum in one Azorean island (Hortal et al., 2010), in this research we present a global view of the archipelago and, more importantly, we are mainly interested to compare the potential distribution of a species that is expanding with that of a species that has been retracting. This might be useful for management, not only in this particular case, but as an example of the potential and also of the limitations involved when trying to model these two opposite situations. A particular type of approach that has not been widely explored in recent work.

We used the modelling approach developed by Hirzel et al. (2002), which is based on the ecological-niche factor analysis (ENFA). The ENFA is a multivariate analysis technique that relies on presence-only data and builds on Hutchinson’s definition of an ecological niche. It was shown to be a reliable and robust method to predict invasive species distribution for conservation purposes in the Azores (Costa et al., unpublished) and it is recommended when absence data is meaningless like in studying invasive or reintroduced species (Acevedo et al., 2007; Cassinello et al., 2006; Hirzel et al., 2001, 2002, 2004; Strubbe and Matthysen, 2009). Moreover, the analysis of the ENFA results is straightforward, easily interpreted and it is available through a user-friendly free software, the Biomapper (Hirzel et al., 2007). All these issues promote links between academics and practitioners.

The specific objectives of our study were two-fold: (i) to study both species ecological preferences and model their habitat suitability (HS) in the Azores by relying on the ENFA modelling approach; and (ii) to find where areas currently occupied by P. undulatum could also be favorable habitat for M. faya based on the modelling results.

2. Materials and methods

2.1. Study area

The Azores archipelago includes nine volcanic islands spanning 615 km and with a total surface area of 2322 km². It is located in the North Atlantic Ocean about 1500 km west from mainland Portugal. The climate is temperate oceanic with a mean annual temperature of 17 °C at sea level; the mean rainfall ranges from 1500 to more than 3000 mm per year, increasing with altitude and from east to west. The natural vegetation includes diverse communities, namely coastal vegetation, coastal and inland wetlands, meadows, peat bogs and several types of native forest and scrub. Islands colonization began in the 15th century and since then several alien plant species have been introduced, affecting native plant communities (Schaef er et al., 2011; Silva et al., 2008; Silva and Smith, 2006).

2.2. P. undulatum and M. faya

P. undulatum was introduced in the 19th century to create living fences around fruit orchards (Droué, 1866). It was able to colonize a wide range of habitats in less than a century (Schaef er, 2003; Sjögren, 1973), while altering the natural transition between the native plant communities between 300 and 600 m a.s.l. (Sjögren, 1973), affecting nature reserves, protected landscapes and several native and endemic plant taxa. Furthermore, tree invaders in the Azores tend to change vegetation structure (see Moniz and Silva, 2003; Hortal et al., 2010). Also, the endangered Azorean Bullfinch is threatened by invasive plants (Bastos et al., 2012), including P. undulatum, and Silva and Tavares (1995) showed that only a few introduced arthropods species are able to survive on the invaders. P. undulatum fruits are used by some native birds like the blackbird, further contributing to its dispersal. Therefore, P. undulatum was considered as one of the priority species for the implementation of control actions (Lourenço et al., 2011; Silva et al., 2008). P. undulatum currently invades up to half of the forested area in the Azores archipelago, which is more than Cryptomeria japonica (26%), Eucalyptus globulus (8%) and Pinus pinaster (2%), the most important forestry species in the Azores (Lourenço et al., 2011). The case of P. undulatum is thus beyond biodiversity conservation only, and should be considered as forest management problem. Several control measures of P. undulatum have been attempted (Gleadow and Narayan, 2007; Rose, 1997; Silva et al., 1999). However, since no resources are available to control the large extension of the invaded area, energetic valorisation could be a solution (Lourenço et al., 2011).

M. faya is an evergreen Macaronesian shrub or tree, considered as a frequent member of the coastal and middle altitude native vegetation, which is also present at the lower range of the Azorean laurel forest, and usually found up to 600 m a.s.l. (Silva and Tavares, 1995; Sjögren, 1973). The beneficial ecological role of this native species in the Azores has been recognized as regards cloud water infiltration, soil nutrient availability and source of food and shelter for birds and endemic insects (see details in Silva and Tavares, 1997). However, Morella stands have been largely invaded by P. undulatum (Machado, 1946; Palhinha, 1944; Ricardo et al., 1977; Schaef er, 2003; Silva and Smith, 2006) and other plant and animal invaders, and were affected by changes in land cover (Silva and Tavares, 1997). According to DRRF (2007), M. faya is currently present in a total of 22% of the forested area in the Azores archipelago but in only 5% of that area, M. faya is the dominant species. To preserve this native species, including the associated flora and fauna, control of invasive plants is thus essential (Silva and Tavares, 1997).

The presence-only data of both species were derived from DRRF (2007), in which cartographic data of 2001 and orthophotomaps of 2004 were used to delimit, in vector format, the forest stands and land cover in the nine islands through visual interpretation within a Geographic Information System (GIS). Between 2003 and 2007, field work was performed to identify the different types of forest stands previously delimited (for further details see Lourenço et al. 2011). We used all the polygons where P. undulatum and M. faya were identified. The vector data was then converted to raster
format of 100 m spatial resolution in order to match the ecogeographical variables used (see below). For *P. undulatum* and *M. faya* we got a dataset of 38,700 and 13,373 cells, respectively. Since the species datasets were large, we were able to randomly divide them into two parts, a modelling dataset and a testing dataset. Accordingly, we used 1/4 and 1/3 of the *P. undulatum* and *M. faya* records as modelling datasets, respectively, and the remaining 3/4 and 2/3 as testing datasets.

### 2.3. Ecogeographical variables

We used ecogeographical variables (EGVs) of three categories: climate, topography and land cover. Climatic variables were selected from the CIELO Model ([Azevedo and Pereira, 1999](#)). In CIELO Model, a raster GIS environment with 100 m spatial resolution is used to model local scale climate variables relying on limited available data from synoptic coastal meteorological stations. More information on the CIELO Model is available through the CLIMATA project at [http://www.climaat.angra.uac.pt](http://www.climaat.angra.uac.pt) and in Azevedo (2003). We used the annual average of the minimum, maximum, mean and range values of temperature (*TMIN*, *TMAX*, *TM*, *TRAG*), relative humidity (*RHRMIN*, RHRMAX, RH, RHRAG) and precipitation (*PMIN*, PMAX, PM, PRAG). In addition, the climatic variables were submitted to a principal component analysis since most of them were highly correlated. The principal components explaining more than 90% of variance in the original variables were held and used alternatively. Those components, used as five alternatives EGVs, corresponded to the first two components extracted from temperature (TPC1-2) and relative humidity variables (RHPC1-2) and to the first component extracted from precipitation variables (PCP).

The topographic and land cover EGVs were acquired from the auxiliary data available in the CIELO Model database, all matching the same spatial resolution of 100 m. To characterize the topography, we obtained the altitude (ALT) as well as the slope (SLP) from a CIELO digital elevation model. Finally, a land-cover dataset was used, which defines six classes: (1) forest, (2) natural vegetation, (3) pastureland, (4) agriculture, (5) barren/barare areas and (6) urban/industrial areas. We tested two different approaches. The land cover classes were sorted in the foregoing order to define an ordinal land cover variable (OLC), from “like forest” (forest) to “unlike forest” (urban/industrial areas). Moreover, distance variables were calculated for each land cover class (DLC1-6). Distance variables express the distance between the focal cell and the closest cell belonging to a given land cover class. In total, 26 EGV were tested and after proficient analyses, we defined three EGV sets (Table 1) for HS modelling.

### Table 1

<table>
<thead>
<tr>
<th>EGV</th>
<th>Unit</th>
<th>EGV set</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Climate</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>TMIN</em>, <em>TMAX</em>, <em>TM</em>, <em>TRAG</em></td>
<td>°C</td>
<td>1</td>
</tr>
<tr>
<td><em>RHRMIN</em>, RHRMAX, RH, RHRAG</td>
<td>%</td>
<td></td>
</tr>
<tr>
<td><em>PMIN</em>, PMAX, PM, PRAG</td>
<td>mm</td>
<td></td>
</tr>
<tr>
<td>PCT1; PCT2</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>PCHR1; PCHR2</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>PPC</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td><strong>Topography</strong></td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>ALT; SLP</td>
<td>m; %</td>
<td>8</td>
</tr>
<tr>
<td><strong>Land cover</strong></td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>DLC1; DLC2; DLC3; DLC4; DLC5; DLC6</td>
<td>m</td>
<td>8</td>
</tr>
<tr>
<td>OLC</td>
<td></td>
<td>8</td>
</tr>
</tbody>
</table>

2.4. HS modelling

The Biomapper 4.0 software was used to run the ENFA modeling approach (hereafter ENFAMA), which consists in a two-step procedure. The first step is the ENFA. It compares the distribution of the species (i.e. the presence-only data) to a reference set (i.e. available area to the species) in the multidimensional space of EGVs previously selected to run the analysis. From this comparison, the so-called global marginality and specialization coefficients are calculated. The former is interpreted as the difference between the conditions used by a species and the average conditions available in the study area. Most often it ranges from zero to one and a large value means the species lives in a very particular habitat. The specialization describes the narrowness of the species niche and any value exceeding unity indicates some form of specialization. In mathematical terms, the comparison is analogous to a principal components analysis, but here the first factor is calculated so that it accounts for all the marginality of the species and the following factors so as to maximize the specialization not explained in the first factor. Consequently, the resulting ENFA factors have an ecological meaning and enables for modelling the species HS for the whole study area through an environmental envelope technique, which is the second step of the ENFAMA. This technique is conceptually very close to the niche theory and it consists in delineating, in the space of the EGVs used, the hypersurface that circumscribes all suitable conditions for the species. As a result, HS is expressed in a continuous raster map of dimensionless scores ranging from 0 to 100. These HS scores do not equal probabilities of presence, but are proportional to the probability that each map cell is used by the species (for a full description of the ENFAMA, see details in Hirzel et al., 2002; Hirzel and Arlettaz, 2003).

We took advantage from the two-step procedure of the ENFAMA. Before the HS modelling itself, we analyzed the species ecological preferences based on the ENFA outputs (marginality, specialization and ENFA factors interpretation). We considered the EGV set 3 for both species. Then, for HS modelling, we combined the available 3 EGV sets together with three environmental envelope-based algorithms (median, geometric mean distance and harmonic mean distance), available in Biomapper, thus yielding 9 HS models. The number of ENFA factors held for HS modelling was defined by comparing the factors’ eigenvalues to the MacArthur’s broken-stick distribution.

2.5. Validation

All the HS models were validated relying on the method proposed by Boyce et al. (2002) and improved by Hirzel et al. (2006), the continuous Boyce curve. This method was chosen because it is a reliable threshold-independent method developed for HS models based only on presence data (Hirzel et al., 2006). It is fairly insensitive to species prevalence and estimates how much the HS model predictions differ from random expectation, which is assumed as a measure of quality of the model. The observed and the expected (i.e. randomly) number of presences are calculated for n HS classes of width W that shift gradually all along the range of HS scores. Then the observed-to-expected (O/E) ratio is plotted against the HS class mean score. Ideally, a good HS model produces a monotonically increasing curve and its goodness of fit is measured by the Spearman rank correlation coefficient, which is the Boyce index (see details in Hirzel et al., 2006).

In our study, the testing datasets were used to calculate the continuous Boyce curves with W = 25 as it is not recommended to use large width values (Hirzel et al., 2006). In order o infer the mean and 95% confidence intervals of the validations results, a bootstrapping procedure was applied in R. From the testing dataset, one thousand replicates were setup with a bootstrapping
sample size of 500, following Efron and Tibshirani (1998). Therefore, the HS models were validated based on the mean continuous Boyce curve and its 95% confidence intervals. Also the mean Boyce index was regarded.

The validation criteria considered were based on the analysis of Boyce indexes and curves shape, as proposed by Hirzel et al. (2006): (i) the standard deviation around the curves should be narrow; (ii) the curves should be linear and ascending; and (iii) the O/E ratio should be high. Only the HS model of the highest robustness and predictive power for each species was selected to be used in further analyses.

2.6. HS models comparison

This analysis regarded strictly the area currently known to be invaded by P. undulatum and intended to define areas likely to be effectively occupied by M. faya. Since the modelled HS scores do not equal probabilities of presence, but are proportional to the probability of use (Hirzel et al., 2006), the HS models could not be compared directly. Therefore, the continuous Boyce curves were used since they estimate how much the HS models differ from random expectation along the range of the HS scores. However, they should not be compared directly either. The deviation from randomness should be used only to compare models of the same species and over the same study area (Hirzel et al., 2006). Therefore, we normalized both continuous Boyce curves in order to reach a maximum value of one. The normalized continuous Boyce curves were calculated as the O/E/M ratio, where M is the maximum O/E value. Then, the HS scores were reclassified in their corresponding O/E/M values and we were able to overlay and compare the HS models. We defined three degrees of expected success for the effective replacement of P. undulatum by M. faya: Low, Medium, and High. For a given cell map, the expected success was Low if the P. undulatum normalized continuous Boyce curve overcame that of M. faya; in the opposite case, the expected success was High. We considered that one curve overcame the other only if their 95% confidence intervals did not overlap. Otherwise, we considered the curves even and the expected success degree was Medium. Finally, the Low degree was assigned to all map cells presenting an O/E ratio below unity for M. faya, regardless the HS of the invader, because any replacement action with M. faya would be ineffective in areas not suitable for it. We considered only the areas of Medium and High degrees as eligible for replacement actions.

3. Results

3.1. Species ecological preferences

A global marginality coefficient (M) of 0.652 and a global specialization coefficient (S) of 1.196 were computed for P. undulatum, while in the case of M. faya, M and S coefficients were 0.960 and 1.470, respectively. This indicates that the difference between the used and the Azorean average environmental conditions is higher for M. faya, and that its niche breadth is narrower than for P. undulatum. Therefore, P. undulatum founds more suitable areas for its spread in the Azores than M. faya, which seems to be more specialized. Nonetheless, both species show quite similar ecological preferences (Table 2). With regard to the marginality ENFA factor, both species are highly and negatively correlated with the land cover (OLC) and highly and positively correlated with the first component of the temperature (TPC1) and of the relative humidity (RHPC1). High values of OLC indicate habitats progressively more different from forest; high values of TPC1 correspond to high values of temperature; and high values of RHPC1 correspond to low values of relative humidity although with a wide annual variation. The altitude (ALT) also seems to be important in both cases since this variable is considerable and negatively correlated with the marginality factor and is highly correlated with the first specialization factor. In the second specialization factor, in general the foregoing EGVs are also important. This means that both species prefer “forest alike” habitats characterized by higher temperature values and wider range of relatively lower values of relative humidity than the average available conditions in the whole archipelago.

![Fig. 1. Validation results of the selected HS models for P. undulatum (top) and M. faya (bottom). Solid black lines: mean continuous Boyce curves; dashed lines: 95% confidence intervals; flat gray lines: O/E = 1 (below this line the model predicts fewer presences than expected by chance); BI: mean Boyce index.](image)

<table>
<thead>
<tr>
<th>EGV</th>
<th>P. undulatum M = 0.652; S = 0.196</th>
<th>M. faya M = 0.960; S = 1.470</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Marg (21.4%) Spec 1 (28.6%) Spec 2 (13.6%)</td>
<td>Marg (30.2%) Spec 1 (27.0%) Spec 2 (15.5%)</td>
</tr>
<tr>
<td>OLC</td>
<td>−0.550 −0.147 0.204</td>
<td>−0.329 0.026 −0.060</td>
</tr>
<tr>
<td>RHPC1</td>
<td>0.492 0.253 0.763</td>
<td>0.531 −0.590 −0.589</td>
</tr>
<tr>
<td>TPC1</td>
<td>0.436 0.299 −0.272</td>
<td>0.542 −0.076 0.689</td>
</tr>
<tr>
<td>ALT</td>
<td>−0.343 0.885 0.465</td>
<td>−0.400 −0.756 −0.026</td>
</tr>
<tr>
<td>SLF</td>
<td>0.329 0.016 0.064</td>
<td>0.199 −0.075 −0.080</td>
</tr>
<tr>
<td>PPC</td>
<td>−0.184 0.175 −0.074</td>
<td>−0.221 −0.104 0.384</td>
</tr>
<tr>
<td>RHPC2</td>
<td>−0.061 0.106 0.245</td>
<td>−0.260 −0.219 −0.058</td>
</tr>
<tr>
<td>TPC2</td>
<td>−0.037 −0.002 0.129</td>
<td>0.036 −0.097 −0.129</td>
</tr>
</tbody>
</table>
Thus, both species avoid the high mountains of the Azores, where temperatures are low and relative humidity and rainfall are high.

Regarding modelling, the HS models of the highest robustness and predictive power for *P. undulatum* and *M. faya* were those yielded with the EGV sets 3 and 1, respectively, both with the harmonic mean distance algorithm. Fig. 1 shows the validation results of the selected HS models. The monotonic Boyce curves predicting both species presence at higher rates than expected by change show that the HS models are proportional to the probability of use and that they have a good predictive power.

The selected HS models of both species are quite similar (Fig. 2). Generally speaking, the higher central regions of the islands are not suitable for both species because they are limited in altitude, which generally corresponds to unfavorable climatic conditions too. These similarities are in line with the results of Table 2. As a result, only 45% of the Azorean land area is potentially suitable (O/E > 1) for either the invasive or the native species. Pico Island is the most suitable one for both species whereas Flores and Corvo islands are the less suitable. However, it is clear that *P. undulatum* finds more suitable sites than *M. faya*, particularly in the islands of Faial, Terceira, Graciosa and Santa Maria, which is related with their divergent global marginality and specialization coefficients.

The modelling results also indicate that both species are not at equilibrium with the environment because their actual distributions (according to DRRF, 2007) do not match their whole potential distributions (according to the HS models). This means that both species can potentially spread to sites not yet colonized, estimated at up to 28% and 17% of the Azores for *P. undulatum* and *M. faya*, considering their respective unoccupied area of O/E ratio above unity.

3.2. Potential habitat for *M. faya* in areas occupied by *P. undulatum*

The selected HS model of *M. faya* reveals that more than half of the area currently invaded by *P. undulatum* is not suitable for this native species (O/E < 1), which turns it a limited alternative to surrogate *P. undulatum*. Nevertheless, taking into account the HS models comparison, it turns out that the *P. undulatum* distribution area could potentially be occupied by *M. faya* in around 13% and 11% with a Medium or a High expected success degree, respectively (Table 3). The comparison of the HS models is shown in Fig. 3. For the sake of legibility, only two islands, Flores and Pico, are shown.

**Table 3**

<table>
<thead>
<tr>
<th>Island</th>
<th>Area of expected success for <em>P. undulatum</em> replacement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Medium and high expected success</td>
</tr>
<tr>
<td>Santa Maria</td>
<td>2</td>
</tr>
<tr>
<td>São Miguel</td>
<td>14</td>
</tr>
<tr>
<td>Terceira</td>
<td>14</td>
</tr>
<tr>
<td>Graciosa</td>
<td>0</td>
</tr>
<tr>
<td>São Jorge</td>
<td>48</td>
</tr>
<tr>
<td>Faial</td>
<td>10</td>
</tr>
<tr>
<td>Pico</td>
<td>38</td>
</tr>
<tr>
<td>Flores</td>
<td>3</td>
</tr>
<tr>
<td>Corvo</td>
<td>0</td>
</tr>
<tr>
<td>Azores</td>
<td>24</td>
</tr>
</tbody>
</table>

Fig. 3 shows that the success of using *M. faya* to reforest the invaded area can be very heterogeneous throughout the different islands. Roughly half of the area occupied by *P. undulatum* in Pico Island presents a Medium or High expected degree of success in its effective replacement by the native species. On the other hand, almost the whole area of Flores Island presents a Low degree. A deeper insight on this is given per island in Table 3.

4. Discussion

According to the results, *P. undulatum* and *M. faya* adapt mainly to the coastal and middle elevation environmental conditions of the Azores, namely to lowlands and forested habitats characterized by relatively high temperature and wide ranges of low relative humidity values. This fact prevents both species from occupying uplands, such as the typical Azorean calderas, the Pico Mountain and the volcanic central ridge of São Jorge Island, which is in line with previous studies on both species (e.g. Hortal et al., 2010;
cess, as shown in Table 3 and Figs. 2 and 3. Therefore, for these reforestation (Table 3). On the other hand, 24% is undoubtedly very relevant to preserve this native species. The similar ecological preferences of both species and the narrowness of M. faya niche make it a plausible but limited option to replace P. undulatum. At best, 24% of the Azorean area currently invaded by P. undulatum should be considered for conservation actions based on M. faya reforestation. One may state that this percentage is insufficient from a biological invasion control standpoint. Specially if considered that other 28% of the whole Azores offers good conditions to its further invasion. However, 24% is undoubtedly very relevant to preserve this native species and its associated flora and fauna.

São Jorge and Pico are the most favorable islands for M. faya reforestation (Table 3). On the other hand, M. faya is less attractive for reforestation in Graciosa, Corvo, Santa Maria and Flores because their most invaded area presented a Low expected degree of success, as shown in Table 3 and Figs. 2 and 3. Therefore, for these cases, as for the remaining islands, other Macaronesian species should be taken into account (e.g. Picconia azorica, Prunus azorica, Erica azorica, Persea indica). Indeed, in our view, several species have to be used together for a full control of P. undulatum invasion. Conditions to allow the combined use of additional Macaronesian species should be created, depending on the island and the particular plant communities to be restored. For instance, Picconia azorica could be used in the reforestation of coastal areas throughout the archipelago (Martins et al., 2011), while Prunus azorica should be used at particular forest types in certain islands (Moreira et al., 2009). However, one should note that we do not propose to remove P. undulatum completely. Firstly, because it is likely not possible due to very steep or inaccessible locations (Lourenço et al., 2011). Secondly, because P. undulatum might play an important role in specific cases. It is used as a source of compost for pineapple plantations in greenhouses and for honey and/or essential oil production (Lourenço et al. 2011). Further, the beneficial ecological function of alien species has been reported in some studies (e.g. Arévalo and Fernández-Palacios, 2005; Geldenhuys 1997; Parrotta et al., 1997). Hence, any control action in the field should be analyzed beforehand.

It was expected that M. faya favorable area could overlap more of the area invaded by P. undulatum since M. faya was described by Drouët (1866) as one of the most characteristic plants of the Azores and it gave the name to Faial Island, which formerly had a considerable cover of M. faya (Silva and Tavares, 1997). However, M. faya present distribution is only a fraction of its past distribution and resulted from considerable changes in land use associated to human activities. Thus, some areas with suitable ecological conditions may no longer be occupied by this native species, which leads the ENFA (as would any other method) to characterize it as a specialist. In practical terms, the foregoing considerations mean that M. faya is probably suitable to replace P. undulatum in more sites than suggested by the results achieved in the present paper, which reinforces the prospects of successful M. faya reforestations. Our results showed that the ENFA is a useful tool in studying species ecological preferences and in the design of control or reforestation strategies, by providing valuable guidelines on where successful interventions might be achieved.

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References
