Original Research Article

Species distribution models with field validation, a key approach for successful selection of receptor sites in conservation translocations

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ABSTRACT

Conservation translocations of threatened species are being widely used to mitigate human impacts. However, their effects are surrounded by some controversy since these actions have often failed to meet planned objectives. Despite the limited number of published studies, existing evidence indicates that a main constraint for the long-term success of translocation actions is the selection of suitable receptor sites. In this study, we present a methodological approach to identify suitable receptor sites that combines the use of species distribution models (SDMs) and *in situ* field validation trials. This method was successfully applied to translocate a population of Critically Endangered *Narcissus cavanillesii*, which was going to be destroyed by the construction of the Alqueva dam (Portugal), the largest dam in Europe. The results of the SDM developed for the target species were biologically validated through *in situ* germination trials in sites with contrasting species suitability values. The population translocated to the site selected with this approach has experienced a stable demographic trend for more than ten years and established new mature plants outside the translocated patches. This methodology, which has proven to be a fast and reliable approach for the selection of appropriate receptor sites for conservation translocations, could be useful in other studies.

1. Introduction

Conservation translocations (IUCN/SSC, 2013), defined as the transfer of any living organism(s) from one place to another by humans, are one of the most complex and controversial issues in conservation (Berg, 1996; Seddon, 2010). Consequently, they have usually been used as a last resource to alleviate the effects of human impacts (Fritz and Chiari, 2013; IUCN/SSC,

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2013; López-Pujol et al., 2006; Shorthouse et al., 2012 among others). Although numerous attempts have been made to create new populations of endangered species by conservation translocation (Falk et al., 1996; Jusaitis, 1997; Jusaitis et al., 2004; Maschinski et al., 2004; Mueck, 2000; Pavlik et al., 1993; Soorae, 2008, 2010, 2011, 2013, 2016, 2018), very few have resulted in sustainable populations with a demonstrable capacity for growth, reproduction and long-term persistence (Godefroid et al., 2011; Guerrant and Pavlik, 1998; Short and Hide, 2015). The limited information on the success of attempts to translocate habitats shows that species assemblages cannot be moved without substantially changing their habitat structure and species composition, thus rendering the translocation unsuccessful in terms of sustaining the original flora and fauna (Bullock, 1998; Gault, 1997; Parker, 1995; Short, 2009).

According to Primack (1996), a successful reintroduction mimics the natural processes of dispersal and establishment. Thus, the more similar the ecological features of the new locality are to the original one, the more chances of survival the population will have. In this sense, site-selection considerations should include physical, biological, logistical and historical criteria, even though what constitutes a suitable site is "far from self-evident" (Fiedler and Laven, 1996). Because we rarely know enough before starting a reintroduction action, it is essential to conduct reintroductions within an experimental framework to understand the underlying ecology of the rare species' distribution, which may influence reintroduction success (Maschinski et al., 2004). According to Pavlik (1996), the success of a translocation can be defined by addressing four goals: abundance, extent, resilience and persistence. This author pointed out that while the former two may be achieved over short time spans (1−10 years), the latter two can only be tested over longer periods (one to several decades) for most species.

As receptor-site selection is one of the critical steps in restoring diversity through species introductions (Fiedler and Laven, 1996), the selection of a new location for a species requires an accurate and specific survey. The fitness of this approach is crucial for the success of the translocation. Biological variables that should be considered can be obtained from the baseline information of the species (pollination vectors, dispersal, competition …), while legal protection and human activities are important logistic criteria. Environmental characteristics of the reintroduction site may be just as important as the traits of the plant to be reintroduced (Kaye, 2009). Therefore, the environmental and geographical range of the target species should be analyzed before conservation translocation.

Species distribution models (SDMs) incorporate sets of data and produce maps that indicate the suitability for the target species in any given place of the territory under study. SDMs have been widely used for several purposes such as: modeling invasions (Draper et al., 2003; Peterson, 2003; Thuiller et al., 2005), analyzing global change effects (Benito Garzón, 2006) and distribution assessment (Guisan et al., 2002; Pearce and Ferrier, 2000; Sérgio et al., 2007). Considering that receptor sites for conservation translocation should be selected in accordance with the ecological requirements of the target species, the use of SDMs can help to determine the most appropriate site (Draper et al., 2004). Microsites selected for conservation trans-locations can have a significant effect on plant translocation success (Jusaitis, 2005), as seen in giant clams (Hart et al., 1999), fishes (Morantz et al., 1987) and amphibians and reptiles (Barker and Ríos-Franceschi, 2014; Sharifi and Vaissi, 2014). A similar situation when dealing with wildlife is the availability of suitable nesting places (Poirazidis et al., 2004; Stoynov et al., 2017). Therefore, when a model is used for site selection, a fine-scale approach should be used to assess the habitat quality of the receptor site. Although little data are available on the effect of new habitats on translocated species, there are a few illustrative studies. For example, Kaye and Brandt (2005) determined that topographic position in a restored wetland affected transplant survival in four rare species (Berger-Tal and Saltz, 2014; Owen-Smith, 2003).

Here, we used the conservation translocation of *Narcissus cavanillesii* during the construction of the largest European dam to test if SDM followed by an experimental validation of the model can be a useful methodology to select accurate receptor sites in reintroductions. The only two populations of *Narcissus cavanillesii* A. Barra et G. López, a Critically Endangered plant in Portugal (Rosselló-Graell et al., 2003), included in Annexes II and IV of the European Community Habitat and Species Directive (Council Directive - 92/43/EEC), were going to be affected by the construction of the Alqueva dam. One of the localities was to be completely flooded and the other would be affected by changes in habitat and human activities. Therefore, a conservation translocation of the population to be inundated was performed in 2001 as part of a series of mitigation activities oriented to minimizing the impact of the dam. The final objective was to avoid the loss of this population by translocating it to a new site with a suitable habitat for the species' persistence. Thus, in this study we specifically asked: (1) Which variables are needed in SDMs to accurately predict new receptor sites? (2) How can we ensure that the SDM statistical validation is correlated to the species' biological performance? And (3) What makes a good statistical SDM fail in reintroductions?

2. Materials and methods

2.1. Target species and area of study

Narcissus cavanillesii is a small geophyte with a height of 4−15 cm and one or two leaves that are not present in flowering bulbs. The geographical distribution range of this autumnal flowering species extends from Algeria and Morocco to Portugal and Spain (Maire, 1952; Valdés et al., 1987). According to the International Union for Conservation of Nature criteria (IUCN, 2001), this species should be classified as critically endangered (CR) in Portugal since 80% of the Portuguese population would disappear if no conservation actions were taken (Draper et al., 2016a, 2016b; Rosselló-Graell et al., 2003). In Portugal there are only two known localities (Ajuda and Monte Juntos; Fig. 1) both reported in the Alentejo region (Malato-Beliz, 1977; Rosselló-Graell et al., 2004), corresponding to the species' western range limit in the Iberian Peninsula.
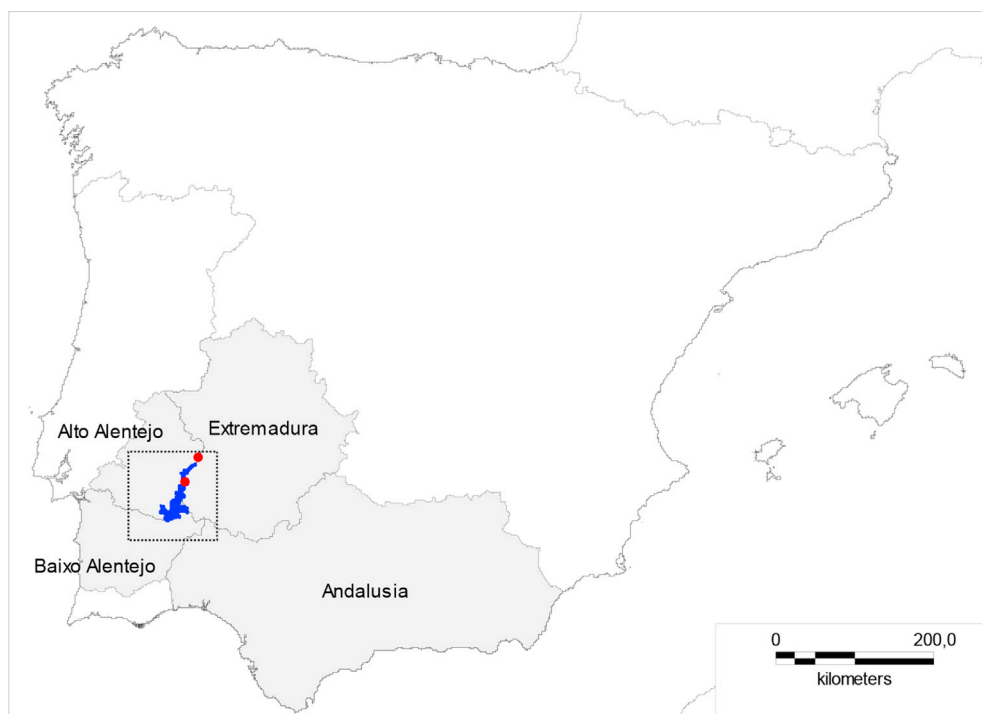
Fig. 1. Location of the Alqueva Dam on the border between Spain and Portugal in the Guadiana River Basin (blue area). Red dots represent the two *N. cavanillesii* populations. Grey areas correspond to administrative areas surveyed to determine the SDM of *N. cavanillesii* in the Iberian Peninsula. The dotted square indicates the geographic window considered for the translocation project circumscribing the entire adjacent area of the reservoir and the two Portuguese populations. Although there are no historical records from the Baixo Alentejo, part of this region was sampled due to its proximity to known populations. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The construction of the Alqueva Dam created the largest dam in Europe, with an area of 250 km^2 and a perimeter of more than 1000 km with a total capacity of 4150 hm^3 (EDIA, 2002). A large area of prime plant habitats on river banks and adjoining areas were inundated, producing serious consequences for the populations of several threatened species protected under both European Union regulations and several conventions signed by Portugal such as the Ramsar Convention (Anonymous, 1994) and the Bern Convention (Anonymous, 1981). On 8 February 2002, the Alqueva Dam gates were closed, and the reservoir started to fill. The flooded areas affected the habitats of several species wherein habitat loss and fragmentation displaced many organisms (Chícharo et al., 2006; Draper et al., 2016a, 2003; Marques et al., 2004; Rebelo and Rainho, 2009).

The two Portuguese populations of *N. cavanillesii* were affected differently by the dam. The Ajuda population was indirectly affected by an increase in human pressure (leisure) and the proximity of the water table, while the Monte Juntos population was directly affected as it was within the area to be inundated. Thus, the only effective option in this case was to perform a conservation translocation.

2.2. Species occurrence and data collection

To characterize the ecological range of the species more accurately, we visited all *N. cavanillesii* populations across its Iberian distribution range during the 2000−2001 flowering period. Primary distribution data were obtained from the herbaria of the Royal Botanic Garden of Madrid (MA), the University of Extremadura (UNEX) and the University of Seville (SEV). Ecological features were recorded following the dataset used in the plant monitoring program of the Alqueva dam (Ballester-Hernández et al., 2000).The Monte Juntos population of *N. cavanillesii* that was to be translocated was located very close to the Guadiana River. It was structured in ten small patches from 0.5 m^2 to 8 m^2 within an area ca. 1.5 ha on skeletal soil (limestone soil) on schist rocks. A mapping survey was carried out to identify the size and location of the patches as well as number of individuals. In October 2000, a detailed survey was carried out in each plot, and all individuals were mapped (Marques et al., 2004).

2.3. Conservation translocation considerations and workflow

The basic guidelines of this conservation translocation followed Fiedler and Laven (1996). To maximize the probability of conservation translocation success, three general aspects were considered in site selection: 1) target species habitat

suitability; 2) proximity to the historical range of the species; and 3) protection status of the receptor site. Species habitat suitability was determined using field data on the Iberian distribution of the species. First, a global SDM was obtained for *N. cavanillesii,* and then this global model was applied to the target Portuguese area. Historical range was obtained from herbarium records. There is reasonable knowledge on the distribution of *N. cavanillesii* in the Iberian Peninsula, but it is difficult to consider the historical range of this species as the Portuguese populations occur at the edge of their global distribution. The factors intrinsic to the Portuguese populations were subsequently incorporated, as they are important in the management of the new location. These factors were distance to the original location (to minimize potential current and future impacts), distance to rivers (to maintain the relationship with water), being within a Site of the Nature 2000 Network and the qualification of undevelopable land in an area outside the final water table of the reservoir. The places with the highest habitat suitability values were sorted according to their distances from the original location. Before making the final selection of the site, landowners should agree with the translocation. Thus, proximity to the two known populations and proximity to rivers were used as proxy criteria for receptor site selection. For this purpose, a layer with surface values inversely proportional to the distance from the original sites was created. Regarding the protection status of the land, the network of protected areas in the region is limited to the sites proposed for the Natura 2000 Network (http://ec.europa.eu/environment/nature/natura2000/index_en.htm), since the nearest Natural Park is located more than 100 km away. As land use changes in areas protected by the Natura 2000 Network are regulated by national authorities, it is reasonable that the future protection of these sites is assured (Anonymous, 1992). The resulting model was also crossed with an anthropological model that considers land uses and protected areas.

The last step was to assess whether the obtained site would be suitable in the long term. As future changes (land use, urban development, new infrastructures …) may negatively affect the species and compromise its long-term conservation, they must also be considered. Thus, current and future SDMs based on land use were intersected to identify sites with suitable conditions for both the present and the future. Future land use changes were estimated based on the type of land use and national regulations. A reclassified land use map was based on CORINE Land Cover produced by the Centro Nacional de Informação Geográfica, CNIG (1:100 000) classified in three categories for *N. cavanillesii* (low, medium or high risk of change).

2.4. Species distribution model

The main limitation of the statistical approach to build an SDM dealing with rare species is their reduced number of occurrence records (only two known sites in Portugal). To overcome this constraint, the geographical window was enlarged to include the overall distribution of the target species in the Iberian Peninsula with a spatial resolution of 500 m. The SDM was then projected at the local scale with a spatial resolution of 25 m.

Climatic and topographic variables were used to build the SDM (see Table 1 for variable details). Climatic variables were generated by applying the predictive models proposed by Sánchez-Palomares et al. (1999), and several bioclimatic indexes were generated from them to discriminate the bioclimatic regions of the target species (Table 1).

Presences of the species in the Iberian Peninsula were obtained from herbarium records, and absences (and pseudo-absences) were obtained from fieldwork and ecological niche factor analysis (ENFA) models, respectively (Guisan and Zimmermann, 2000; Hirzel et al., 2002). The Iberian pseudo-absences were randomly generated within the ENFA multi-space excluding buffer zones to avoid spatial correlation. The procedure followed is similar to principal components

Table 1
Name, code and origin of the variables used in this study.

Variable	Code	Origin
Altitude (m)	ALT	Downscaled from GTOPO30 to the Iberian distribution and from 1:25 000 vectorial cartography provided by EDIA for the Alqueva area.
Aspect	ASPECT_RC	Derived from ALT and reclassified according Draper et al. (2003)
Slope (°)	SLOPE	Derived from ALT
Longitude (m)	X	Obtained from ALT
Latitude (m)	Y	Obtained from ALT
Monthly rainfall (mm)	RAIN_XX	Sánchez-Palomares et al. (1999), where XX: 01 = January to 12 = December
Annual rainfall (mm)	RAIN_13	Sánchez-Palomares et al. (1999)
Max. monthly temperature (°C)	TMAX_XX	Sánchez-Palomares et al. (1999), where XX: 01 = January to 12 = December
Max. mean annual temperature (°C)	TMAX_13	Sánchez-Palomares et al. (1999)
Mean monthly temperature (°C)	TMEA_XX	Sánchez-Palomares et al. (1999), where XX: 01 = January to 12 = December
Mean annual temperature (°C)	TMEA_13	Sánchez-Palomares et al. (1999)
Min. monthly temperature (°C)	TMIN_XX	Sánchez-Palomares et al. (1999), where XX: 01 = January to 12 = December
Min. mean annual temperature (°C)	TMIN_13	Sánchez-Palomares et al. (1999)
Angot Index	ANGOT	Angot (1906)
Dantin-Revenga Index	DANTIN	Dantin and Revenga (1941)
Emberger Index	EMBERGER	Emberger (1932)
Gams Index	GAMS	Gams (1931)
Giacobbe Index	GIACOBBE	Giacobbe (1938)
Lang Index	LANG	Lang (1915)
Martonne Index	MARTONNE	de Martonne (1926)

analysis, involving a linear transformation of the environmental space into orthogonal factors (Phillips et al., 2006). Subsequently, pseudo-absences were randomly selected out of the suitable space. The buffer radius was determined by the lag distance at which the semi-variogram reached the sill value (autocorrelation is essentially zero beyond this distance). The lag distance in our case was 100 km.

The species distribution model was calculated according to a logistic regression (Hosmer and Lemeshow, 2000) using an equivalent pool of *N. cavanillesii* presences and absences.

A multiple linear regression (MLR) was applied using only the resulting significant variables:

$x = a_0 + a_1 x_1 + a_2 x_2 + a_3 x_3 + \ldots . + a_n x_n$

Where x is species' occurrence, a_0 is the intercept value, $a_1.., a_n$ are the regression coefficients and $x_1.., x_n$ are the independent variables.

The resulting model was then adjusted to a logit transformation (Hill and Domínguez Lozano, 1994) by:

$$E(\text{logit})(Y)) = E(p/q) = \frac{e \sum x}{1 - e \sum x} + \varepsilon$$

Where Y is species habitat suitability; p is the probability of one of the states of the binary variable; and q is the complementary probability. The logit transformation ensures that the predicted probability will be continuous between 0 and 1. Variable selection was performed in both directions (stepwise and backward). Only significant variables were considered to build the model ($p < 0.05$). The Akaike information criterion (AIC) (Sakamoto et al., 1986) was used to select the most parsimonious combination of significant variables. The fitness model was assessed considering 75% of the data and validated with the remaining 25%. All analyses were performed in raster format using Idrisi (v14.0.2) and Statistica 6.0.

2.5. SDM field validation

As germination, establishment and the number of breeding individuals are important elements for population success in the genus *Narcissus* (Blanchard, 1990; Marques and Draper, 2012a), the appropriateness of the final location of the receptor site determined by the SDMs was validated by *in situ* germination trials. These biological trials aimed to verify the habitat suitability of the selected receptor site. Three groups of habitat suitability classes were considered to generate sampling zones for germination trials, based on SDM results. The class with maximum habitat suitability corresponded to sites with suitability values equal to or greater than those of sites where *N. cavanillesii* is present (Ajuda and Monte Juntos — original locality). The remaining two classes had subsequently lower habitat suitability values and were determined according to frequency values, thereby ensuring that each class had the same representation in area (number of pixels). The rest of the territory, with even lower habitat suitability values, was not considered.

This categorization was crossed with geographical stratification to ensure that the model was evaluated throughout the study area. The three watersheds in the area, Degebe, Upper and Lower Guadiana, were considered (Fig. 2).

Using these two criteria (habitat suitability and geographical stratification), six sites were randomly selected for each habitat suitability class for the germination trials with two points in each basin sector, plus one control in the non-affected Ajuda population and another in the selected receptor site near Monte Juntos. The population of Ajuda was used as control because host an important population of *N. cavanillesii* and the selected receptor site near Monte Juntos to get a projection of the fitness. Thus, a total of 18 points plus two control points were used to validate the SDM.

At each of the 18 test points, we placed a germination assay consisting of six blocks (replicates) of 25 seeds each. In each block seeds were spaced 3 cm apart from each other. Seeds used in the germination trials were collected in early December from the Ajuda population. Germination trials were conducted in December—January to coincide with the natural germination timing of the species. Six weeks later, the trial plots were extirpated, and germination was determined by examining the seeds in the soil samples. Extirpation avoided the potential dispersal of the species to places where seeds had been sown for experimental purposes. Germination rates were arc-sin transformed and then analyzed with an ANOVA ($p < 0.05$). The Scheffe test ($p < 0.05$) was applied for mean comparisons. Linear regressions between seed germination rate and habitat suitability were performed for each basin to determine the basin where *N. cavanillesii* had a greater fit to the SDM.

3. Results

3.1. Species distribution model

The set of original variables was reduced to 10 final significant variables. Most of them were significant at $p < 0.001$ (RAIN_07, RAIN_08, TMIN_13, TMEA_03, TMEA_08, TMEA_09, TMEA_12, ANGOT), except ASPECT_RC and RAIN_09 which were significant at $p < 0.01$ and $p < 0.05$, respectively.

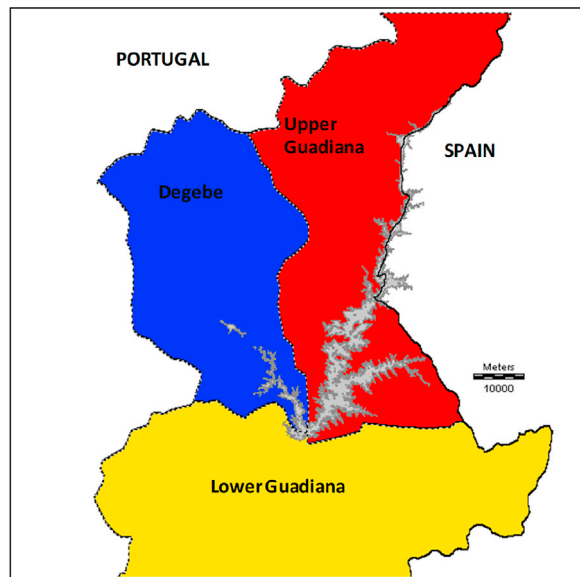The resulting coefficients of the logistic model of *N. cavanillesii* were:

Fig. 2. Geographical area considered for the translocation. The three basin sectors used to stratify the sampling sites are indicated by different colors and the reservoir shape is represented in grey. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

[SUITAB] = 40.570−3.137*[TMIN_13]-0.080*[ASPECT_RC]-1.021*[RAIN_07]+0.788*[RAIN_08]-0.016*[RAIN_09]+2.392* [TMEA_03]-1.695*[TMEA_08]-1.462*[TMEA_09]+2.960*[TMEA_12]-16.850*[ANGOT]

The AIC of this model was 4799.39. The percentage of correct attributions for absences ($n = 5041$) was 85.6% for training data and 98.1% for testing. The percentage of correct attributions for presences *(n = 5625)* was 93% for training and 83.8% for testing with $X^2(10) = 6287.0$ and $p < 0.001$. The results of the SDM after a logit transformation are represented in Figure S1, and the projection to the local study area is shown in Fig. 3. The closest and most suitable site that met all the climatic, ecological and anthropic conditions was located just 1.5 km north at a height 30 m above the original population.

3.2. Field validation

Mean habitat suitability and standard deviation of *N. cavanillesii* populations was 0.999632 ± 0.000017. The highest species suitability class represented an area of 303.18 km^2. The middle and lower species suitability classes were defined by an equivalent area (302.88 km^2 and 303.08 km^2, respectively) with probability ranges from 0.999607 to 0.999571 and from 0.999550 to 0.999571, respectively (Fig. 4).
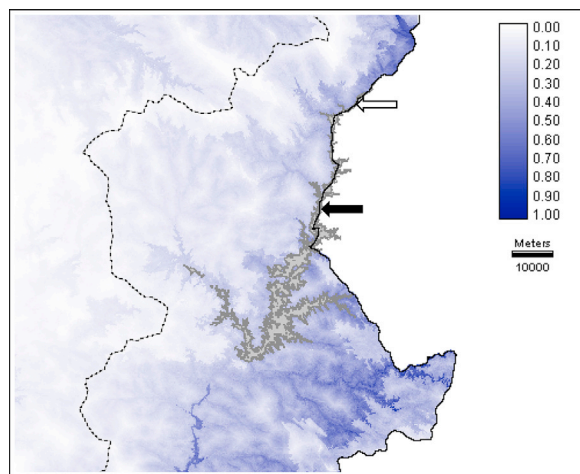

Fig. 3. Local projection of the SDM of *N. cavanillesii* in the target area before the overlay of local parameters. Arrows indicate natural populations of *N. cavanillesii*, the white arrow indicates the location of the Ajuda population (control) and the black arrow indicates the location of the translocated population (Monte Juntos).
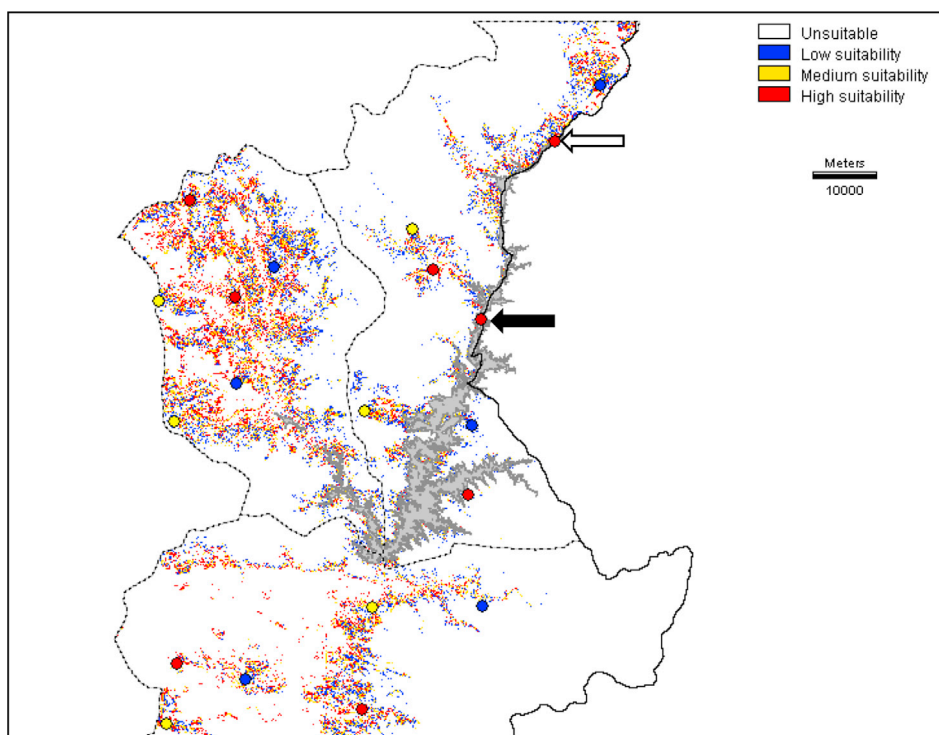
Fig. 4. Ranges of species suitability in the study area and distribution of the 18 localities where the *in situ* germination trials were performed. Six sites were selected in each basin, two for each probability class plus two tests in the Ajuda populations and the potential receptor site near Monte Juntos (red, yellow and blue dots correspond to sites with high, medium and low habitat suitability, respectively). Arrows indicate natural populations of *N. cavanillesii*, the white arrow indicates the location of the Ajuda population (control) and the black arrow indicates the new location of the Monte Juntos population (potential receptor site). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The *in situ* germination percentages obtained for each point were consistent with the probability of species occurrence assigned by the SDM, and the Scheffe test found significant differences between the high habitat suitability points and the medium and low habitat suitability points. (Table 2).

The linear regression between germination response and the SDM indicates the accuracy of the model with respect to environment limitations, at least at the germination stage (Fig. 5). A low fit was obtained in the area furthest from the original location ($R^2 = 0.13$) in the Lower Guadiana basin, and an intermediate fit ($R^2 = 0.60$) was obtained in the Degebe area. The maximum germination rate (94%) and the highest fit value ($R^2 = 0.83$) was obtained in the Upper Guadiana basin where the plants come from. The selected site near Monte Juntos had both one of the highest suitability values and a high germination rate (Fig. 5).

4. Discussion

4.1. Which variables were important to infer the suitability distribution of Narcissus cavanillesi?

As an autumnal blooming geophyte, *N. cavanillesii* requires a particular rainfall regime during the months prior to flowering. According to the model obtained for this plant, it requires little rainfall in July and September but benefits from rainfall in August. The bulb needs to be rehydrated after a dry summer to prepare for the flowering season, and some affinity is expected between species and rainfall. *N. cavanillesii* is related to areas with low mean temperatures in August and September (just before flowering), but warmer temperatures in December and March (the photosynthetic period in which leaves have emerged from the bulb and are operational)(Marques and Draper, 2012b). The negative relationship with mean annual minimum temperature is consistent with a species from the lowlands of the southern Iberian Peninsula and North Africa where temperatures are relatively constant throughout the year. This pattern of precipitation and temperatures is also supported by the Angot index which indicates that the species takes refuge in less continental areas in the south of the Iberian Peninsula like lowlands near the sea coast or river valleys. The model also detects a slight role of the ground aspect where the plant would occupy flat spaces (without defined exposure) or spaces slightly oriented to the north (Marques et al., 2004).

Our site selection procedure did not take into account the effect of anthropogenic factors or future climate change on the *N. cavanillesii* population because the new site was very close to the original population (1.5 km). Thus, the climate change that will take place at the new site will have the same effect on the population than if it had not been translocated. Modeling the

Table 2

In situ germination percentages of *Narcissus cavanillesii* seeds obtained at 20 sampling sites along the three basin sectors of Guadiana river to validate the niche model. At each site, sample size was 150 seeds, distributed in 6 blocks of 25 seeds each. Items with the same letter do not differ significantly (Scheffe test, $p < 0.05$).

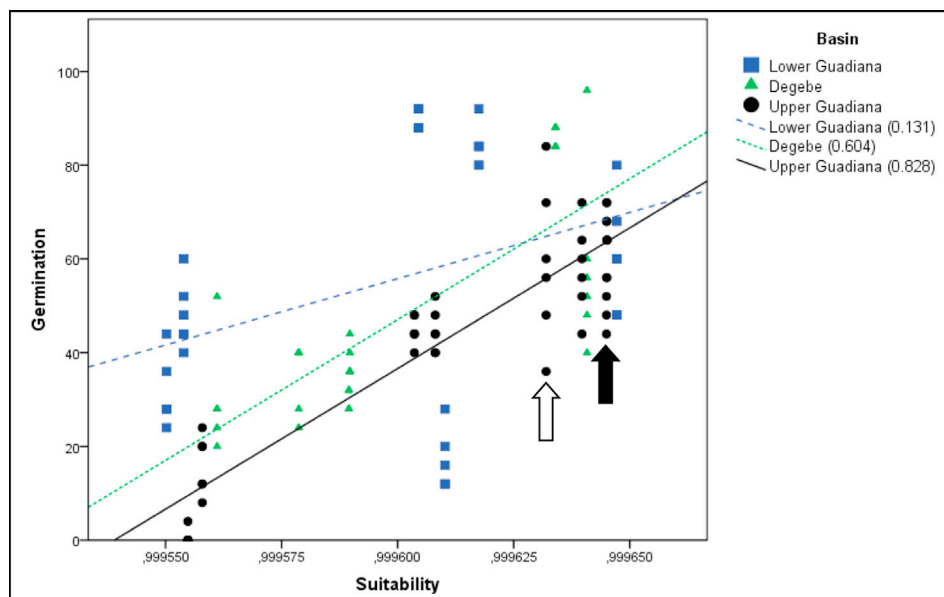| Species suitability class	Germination (%) (average ± sd)	Mean germination within category (%)
High	61 ± 12^g	71 ± 14
High	65 ± 5^g	
High (receptor site near Monte Juntos)	$67 \pm 11^{f,g}$	
High	$59 \pm 20^{f,g}$	
High	$58 \pm 10^{f,g}$	
High	87 ± 2^h	
High (Ajuda)	69 ± 17^g	
High	84 ± 4^h	
Medium	17 ± 6^b	44 ± 23
Medium	$45 \pm 5^{d,e}$	
Medium	89 ± 2^h	
Medium	$45 \pm 3^{d,e}$	
Medium	$38 \pm 3^{c,d,e}$	
Medium	30 ± 2^c	
Low	$35 \pm 7^{c,d}$	27 ± 17
Low	30 ± 11^c	
Low	16 ± 6^b	
Low	0 ± 2^a	
Low	$48 \pm 7^{e,f}$	
Low	31 ± 7^c	

Fig. 5. Linear regressions of germination percentage versus habitat suitability for each basin (blue: Degebe; green: lower Guadiana and black: Upper Guadiana). Greater data dispersion is observed in the Degebe basin, while the Upper Guadiana has the greatest fit between seed germination and habitat suitability. R^2 values are indicated in parentheses. Arrows indicate the position of natural populations of *N. cavanillesii*; the white arrow indicates the Ajuda population (control) and the black arrow indicates the potential receptor site of the Monte Juntos population. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

effects of global warming on rare species requires a fine scale to predict the places where possible refugia lie (Maschinski et al., 2006). When the conservation translocation was carried out, there was no information available on potential microclimatic changes derived from the influence of the dam and, therefore, they could not be considered in the model.

Despite the current proliferation in the use and diversity of modeling algorithms and the ease of access to biological data and explanatory variables, it is worthy to note that in 2000 the situation was very different. If we look at the algorithms available at the time, there were obviously GLMs, although they were not commonly applied to model the distribution of species, let alone rare species, since they generally require more than 30 records to assume normality. Algorithms such as GARP (Stockwell, 1999) had just appeared and generally required 10 records to achieve acceptable adjustments. The year 2000

was 6 years before the use of Maxent was generalized (Phillips et al., 2006) and then became one of the most widely used algorithms for its robustness and versatility (Elith et al., 2006, 2011). Biological collections were almost authentic, impregnable fortresses in 2000, with a very low level of computerization and the total absence of collaborating networks. GBIF existed only as an idea of the future, very far from its current functionalities and potentialities, formally instituted in 2001. Access to descriptive variables was at best based on atlases that could be vectorized or rasterized, Worldclim for example would arise in 2005 (Hijmans et al., 2005).

4.2. Experimental validation of SDM to confirm habitat idoneity of receptor site

Great importance has been given to the statistical validation of ecological models. Different approaches have been used such as the analysis of residuals (Sakamoto et al., 1986; Legendre and Legendre, 1998), by comparing model predictions to real observations and using the area under the curve (AUC) of a receiver-operating characteristics (ROC) plot (Elith et al., 2006; Lobo et al., 2008). These approaches help determine the degree of fit between the initial data and the models used, but do not actually assess the fit between the model and the real environmental requirements of the species. This requires the use of specific field or lab experiments. Each step in important conservation actions like translocations should be evaluated, as success has often been uncertain (Bullock et al., 1996). In this way, future actions can be adjusted.

The use of germination tests to establish the fit of the model from a biological perspective can help determine the appropriateness of the selected receptor site. However, to our knowledge, the only other study to do this was Jusaitis et al. (2004) who used germination tests in *Brachycome muelleri* as part of the experimental validation of the model and to test certain scenarios. It should be noted that germination tests only evaluate a small part of the plant life cycle and that the best approach would be to monitor the response of the plant through its full life cycle. In any case, the assessment of this stage of the cycle is already a significant improvement since most studies do not carry out any *in situ* validation at all. While we evaluated each model and got a good fit to the response of the species, we should not forget that this is just a model, a simplification of reality. The ideal approach would be to validate the model for each critical stage of the species' life cycle (germination, establishment, flowering, fecundity …) in advance. However, this would take several years in some species, which is not feasible due to lack of resources or the more urgent need to carry out the conservation translocation.

Analysis of the regression values suggested a high fit of the model in the Upper Guadiana Basin. The coefficient of determination obtained in the Degebe Basin was $R^2 = 0.60$. This value is high compared to the value obtained for the Lower Guadiana. It is noteworthy that the main physical separation between the Upper and Lower Guadiana is the Sierra de Portel by Moura, while the separation between the Degebe basin and the Upper Guadiana is much less apparent.

Furthermore, the analysis of variance and subsequent post-hoc mean comparisons performed with the complete set of data showed that seed germination was significantly greater in locations ascribed to the high habitat suitability class than in locations ascribed to medium and low habitat suitability classes. Overall, these results validate the appropriateness of the SDM.

With all the limitations of the calendar, techniques and knowledge of the species, the models created allowed an accurate selection of the receptor site, in a conservation translocation process that has been shown to be operational and well executed (Draper et al., 2016a, 2016b). We monitored the translocated population for more than 10 subsequent years and found a progressive increase in the number of flowering plants. Starting with a minimum of 33% of the original number in 2001 (immediately after translocation) (Draper et al., 2016a, 2016b), the population regained its original number of flowering plants and, for the first time in 2010, census values exceeded the percentage of mature individuals measured before conservation translocation. In the years after 2010, the number of mature individuals increased slightly, and new individuals were even found flowering outside the translocated patches (Draper et al., 2016a). The finding of new individuals outside the translocated patches suggests that the new site fulfils all the needs of *N. cavanillesii* and that the procedure followed was a successful approach. That confirms that the receptor site has suitable conditions for species germination and the establishment of adult plants.

4.3. Integration of SDMs in conservation translocations: why good statistical models fail in reintroductions?

Translocations have been portrayed by some as a means of reducing the impact of human development (mitigation), but in reality they can only partly make amends (as incomplete compensation) (McLean, 2003). Lack of knowledge, short reaction times and limited data are common features in translocation actions. All this is compounded if we add the difficulty of working with rare species. By the nature of their rarity, rare species cannot be considered at large spatial or community scales because they are, as Gaston (1994) suggests, statistically problematic. However, this constraint can be overcome by iterative modeling processes (Guisan et al., 2006).

Another issue is the scale and resolution (usually spatial but in some cases also temporal) of the descriptor used to build the model and its capacity to describe a local situation. A fundamental point is that there is no single correct scale on which to describe species distributions (Wiens, 1989). Choosing the correct scale of description is not the problem, but rather recognizing that change takes place on many scales at the same time (Levin, 1992). Recent studies have shown that a multi-scale approach is needed because habitat suitability is related to different factors operating at different spatial scales (Pearson and Dawson, 2003; Store and Jokimäki, 2003). Thus, a major difficulty in distribution modeling is that models built for one small area may not apply to other areas. Similarly, models built for a large area may have weak local predictive power due to

differences in the available or selected habitats or to unmodeled processes that may dominate species distribution patterns at the local scale (Osborne and Suárez-Seoane, 2002). Both scale and spatial resolution should be increased for rare species, as they mostly have a narrow ecological amplitude and often depend on specific interactions of particular environmental variables (Jelaska et al., 2003). Thus, a finer data resolution may provide more detailed information but it is also more difficult to produce or access and not always result on the most reliable outcomes (Fernández and Hamilton, 2015). The major challenge therefore, is to identify the threshold resolution at which predictor variables correctly describe local conditions and biotic interactions which play an important role in defining species' distribution (Manzoor et al., 2018). Bioclimatic and biophysical variables are usually incorporated in SDMs however, an injudicious use of these variables without considering factors like species' ecology, scale of study and optimal grain size is questionable (Manzoor et al., 2018; Wang et al., 2016). Special attention must be paid to the incorporation and final selection of the variables to avoid spurious correlations that actually have nothing to do with the environmental factors that really constraint the distribution of the species.

Biotic interactions, such species community (i.e., microfauna, endobiont bacteria, mycorrhizae, etc., both in the donor and the receptor sites) or pollinator diversity, are still lacking in most SDMs as predictor variables. Such interactions can be determinant for the adaptation to the new location and the final success of the translocations independently of the statistical parameters. Even more when most translocations are performed with individuals that have grown in nurseries. Once again not all interactions are well understood and if known it is not common to have spatially-explicit information about them. In this sense, when possible, it is advisable to perform a habitat translocation (Box, 2003), as we did in this case, where biotic interactions existing in the soil are moved along with the plants, and the impact of the adaptation to the new site is minimized.

Although GIS and modeling techniques have already been incorporated in the selection of receptor sites (Cilliers et al., 2013; Draper et al., 2016a; Morantz et al., 1987; Piana and Vargas, 2018; Sharifi and Vaissi, 2014), the biological validation processes that ensure the reliability of the models and its suitability continue to be scarce.

5. Conclusions

Based on the obtained results, we conclude that the use of SDM generated to accommodate translocated populations is a valid procedure both statistically and biologically if accurate variables are introduced in SDMs. We recommend the use of models to select new receptor sites for conservation translocations, but we also encourage some kind of biological validation of such models prior to translocation. There are at least three major considerations that should be followed when implementing SDMs in conservation translocations: (1) Scale of the phenomenon and data-set quality to be used; (2) Variables used in the models should have biological meaning and be statistically significant; (3) Models should be validated biologically considering the critical life stages of each species (e.g., germination, nesting, feeding, establishment). In this study, germination proved to be an independent way to validate the SDM in *N. cavanillesii* and directly provide information on the species' behavior.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00653.

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