The effects of climate warming and urbanised areas on the future distribution of *Cortaderia selloana*, pampas grass, in France

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Summary

The spread of many invasive plants could be facilitated by their presence in urban areas that may act as dispersal centres and by climate warming. *Cortaderia selloana*, pampas grass, is native to South America and raises considerable concern worldwide as an introduction. We used Maxent niche modelling, based on occurrence records and on a set of simulated occurrence points with high probability of presence in urbanised areas in France, where the species was introduced and is still planted. We calibrated the model with current climate data coupled with several habitat variables and used it to predict range shifts of *C. selloana* under four climate change scenarios (RCP) for 2060. The results were consistent with the known ecology of the species and showed that the most important variables that explain the current distribution in the introduced area were mean annual minimum temperatures, sandy habitats, disturbed habitats and urbanised areas. While the species already occupies large areas along the western and Mediterranean coasts, the models predicted an expansion northward and inland to the east under future climates. The area of suitable habitats could increase by up to 69% under the RCP 8.5 climate scenario in 2060 and by 116% with the extra occurrences in urban/suburban areas. This latter scenario suggests that areas like public and private gardens or urban parks, where the species is currently cultivated, could contribute to increase the invasion risk under climate warming. The results provide predictions of potential environments for the species, which can be helpful for anticipating its spread.

Keywords: species distribution model, Maxent, invasive species, biological invasion, climate envelope, habitat suitability, ecological niche model.

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Introduction

Predicting the spread of invasive plant species in a world where temperature, atmospheric carbon dioxide, precipitation, urbanisation and land use are rapidly changing, is a major challenge (Bradley, 2016). Growth and spread of invasive plants may be facilitated or accelerated by climate change, particularly by the increase of temperatures. The ecological impacts of some invasive species and weeds, and their rapid spread, have highlighted the need for modelling their future distribution (Pyšek *et al.*, 2012). Species distribution models (SDM) and ecological niche models (ENM) are increasingly used to model ecological niches and predict suitable habitats and spread of plants beyond their native ranges (Wan *et al.*, 2017). Effective measures to control invasive weeds require climate models coupled with other environmental variables that are able to accurately predict the potential distribution of invasive species (Costa *et al.*, 2013). Running these models with climate change scenarios allows ecologists to anticipate future changes in the distribution of species. In this respect, one of the most utilised approaches is maximum entropy modelling or Maxent (Phillips *et al.*, 2006). This model is increasingly used because it can manage species presence-only data and successfully maps the distribution of native and invasive plants (Phillips & Dudik, 2008).

In the present study, we focused on the future distribution of *Cortaderia selloana* (Schult. & Schult. F.) Asch. & Graebn (Poaceae) (pampas grass) in a climate change context. This species is native to southern South America (Argentina, Brazil, Chile and Uruguay) and was introduced to Australia, Europe and North America as an ornamental plant in the middle of the 19th century (Lambrinos, 2001). The plant has since escaped from private and public gardens or urban parks, colonising a great variety of natural habitats across the world, and can now be found in Australia, Hawaii, New Zealand, South Africa and along the west coast of the United States. It has spread extensively in Europe, particularly in France, Great Britain, Italy, Portugal, Spain and Turkey. Like its congener *C. jubata* (Lem.) Stapf, which has been listed as highly invasive in Europe (Tanner *et al.*, 2017), *C. selloana* is one of the most aggressive invasive species worldwide, and in some areas such as Australia, one of the fastest spreading weed (Parsons & Cuthbertson, 2001). However, few studies exist on this species, and to our knowledge, there are none concerning its distribution and environment relationships. *Cortaderia selloana* is a gynodioecious grass, although it functions mostly as a dioecious species. One plant can produce between 100 000 and 1 million seeds per year that can be wind-dispersed probably over 33 km (Domenech, 2005). *Cortaderia selloana* preferentially grows in wet habitats under Mediterranean climate (Herrera & Campos, 2006), but has a broad ecological tolerance facing prolonged water stress, cold winters and hot summers (Domenech & Vila, 2006). Under temperate climate (western France), *C. selloana* can also grow in dry places, because there is no summer drought. In its native range, *C. selloana* can regenerate and recolonise after fire (Sirolli & Kalesnik, 2011). The plant easily colonises open habitats (heathlands, dunes, coastal zones), roadsides and urban ecosystems, particularly on disturbed soils (Pausas *et al.*, 2006). It can rapidly form dense monospecific populations of large tussocks, often reaching 3 m high, outcompeting many native species. In addition, dense populations of *C. selloana* increase the risk of fire and alter soil biogeochemical cycles (Domenech & Vila, 2006).

This grass was first introduced to France in the Montpellier Botanical Garden in 1857 and was commercialised after 1874 (Bossard *et al.*, 2000). It has been largely available and sold extensively in garden centres between 1960 and 1980. Its spread began in the early 1990s from a first set of locations in southern, south-eastern and western France, which probably coincided with the first locations of plantation and cultivation, then from a second set of locations in the south-western part of the country. In France, as in other countries, *C. selloana* and many of its cultivars are still available commercially and are frequently planted in private gardens, urban parks, public squares, on roundabouts and roadsides, all representing potential dispersal centres (Charpentier *et al.*, 2006). However, these urban or roadside occurrences are rarely taken into account in botanical distribution databases, because urban habitats are often under-investigated by plant ecologists who focus mainly on natural sites (Kadmon *et al.*, 2004).

Here, we aimed to model the potential distribution of *C. selloana* in France under different climate change scenarios with a data set of known *C. selloana* occurrence. We confront these predictions with others simulations, based on a scenario with extra occurrences in urban areas that are often under-sampled during naturalist surveys and that we estimated to be more representative of the current distribution. Running models with a simulated data set is useful to test model performance and to explore different scenarios (Warren & Seifert, 2011). The potential distribution map of invasive species is a crucial early warning tool for designing control plans (Hussner *et al.*, 2016). Therefore, we produced distribution maps for France using Maxent to model the current and future distribution of the species, testing four Representative Concentration

Pathway (or RCPs) climate scenarios coupled with several landscape and habitat variables. We focused on France as a study area because the species has rapidly spread during the last 25 years in this country and because accurate data sets of its occurrences were available.

Material and methods

Species occurrence data sets

We used a national plant database with the collaboration of the Service de co-ordination technique des conservatoires botaniques nationaux (SCTCBN), under the auspices of the AFB (Agence Française de la Biodiversité). This database contains 1998 records obtained from botanical surveys conducted by trained observers over 5 × 5 km cells distributed across the country. This set of occurrence data was named scenario A (Fig. 1), whereas the set with extra occurrences was named B (detailed below). Species distribution models gain in accuracy and power when the range of the studied species is close to equilibrium under the current climate (Vaclavik & Meentemeyer, 2012). A preliminary task was therefore to test whether the species had reached equilibrium in France (see details in Appendix S1)

Habitat and climate variables in France

We extracted habitat variables from the CORINE Land Cover (2012) and BD TOPO® databases (IGN). All data were categorised (Appendix S2) and converted to raster format with a resolution of 5 × 5 km using ArcGIS 10 (Environmental Systems Research Institute Inc., 380 New York Street, Redlands, Calicornia, USA). Each variable was attributed to each 5 × 5 km cell depending on the closest distance between the centroid of the cell where the species was recorded and the nearest entity of the habitat variable. For the current climate data, we selected fundamentals climate variables from the Bioclim database (Fick & Hijmans, 2017; World Climate: http://www.worldclim.org/version2), downscaled at 1 km² resolution and aggregated here at 5 × 5 km. We used the average monthly climate data for minimum, mean and maximum temperatures and for precipitation for the period 1970–2000. We identified collinearity and estimated the importance of the effect of multicollinearity among explanatory variables (see details in Appendix S3).

Projections of future climate were obtained from the latest scenarios of greenhouse gas concentrations in the atmosphere produced by the Intergovernmental Panel on Climate Change (IPCC). Future climate conditions were predicted from four RCPs scenarios: RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5. Each RCP is based on possible radiative forcing values until 2100, of +2.6, +4.5, +6.0 and +8.5 W m^{-2}, respectively, and corresponds with an increase in global mean surface air temperature of +1.0, +1.4, +1.3 and +2.0 °C for the period 2051–2060. Future climate anomalies assessing the changes in temperatures and precipitations between the 2051–2060 and 1970–2000 periods for each RCP scenario were both downloaded from the KNMI Climate Change Atlas (i.e. climate predictions averaged among all GCM as described in van Oldenborgh *et al.* (2013); https://climexp.knmi.nl/plot_atlas_form.py) and then downscaled at 1 km² resolution using bilinear spatial interpolation. Future climate anomalies were added to the current WorldClim climate layers (1 km² resolution) to infer future climate conditions during the 2051–2060 period. Finally, future climate conditions were aggregated at 5 × 5 km in order to match the grid of species observations.

Species distribution modelling

We used Maxent, version 3.3.3k (Phillips *et al.*, 2006), with distribution data from the native range and France to predict the probability of *C. selloana* occurrence, map its potential suitable habitats and study
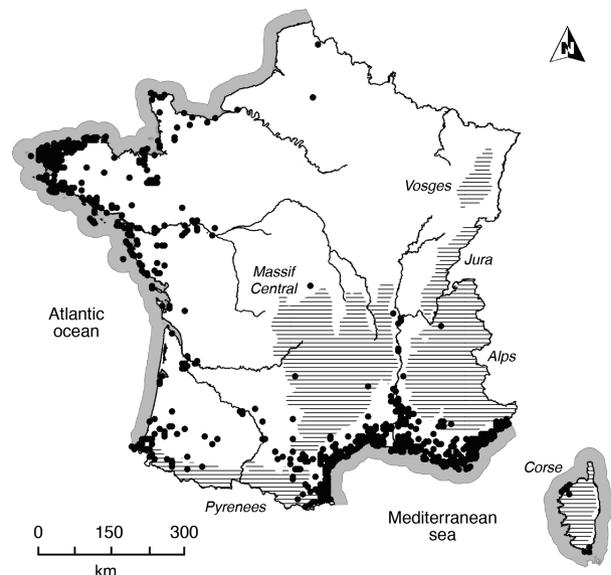
Fig. 1 Map of occurrence data of *Cortaderia selloana* (from Fédération des Conservatoires Botaniques Nationaux) in France. Main river corridors are represented as well as mountains (dashed lines).

relationships with the environmental variables. We first modelled the climate envelope of *C. selloana* in its native range, where the species distribution is presumably at equilibrium. For this, we used 113 occurrences from the Global Biodiversity Information Facility (GBIF). To compare native and introduced ranges of climatic variables, the modelling procedure was the same as it was for France (except the use of scenario B; see below).

Because the current distribution of invasive species in an introduced area may not reflect its whole ecological niche, especially when the species is not at equilibrium, the models were fitted using both native and invasive range data together following the Minxent procedure (Merow *et al.*, 2016). With this procedure, first, the bioclimatic envelope was modelled from the occurrence data and bioclimatic variables of the native range. Then, models in France were made with occurrence data, bioclimatic and habitat variables from France, by considering the native bioclimatic envelope introduced as background (as specified by the Minxent procedure). The same procedure was used to predict potential future distributions in France under future climate (RCPs scenario) and habitat (considered unchanged from today) conditions.

Models were trained using a random selection of 75% of occurrences and then tested on the remaining 25% to test the predictive performance of the model. When sampling effort is not equal across space, it increases spatial autocorrelation (SAC) of sampling sites which biases model performance and outputs. Therefore, we applied a *spatial filtering* on the occurrence data set, that is the procedure by which spatially autocorrelated points are removed using the SDMtoolbox (Brown, 2014), to reduce SAC and to increase the model performance (Boria *et al.*, 2014). The multiple rarefying distance from 2 to 10 km was selected; 10 km was the default value based on high spatial heterogeneity measured for moderately mountainous to mountainous regions (see Boria *et al.*, 2014; and references therein). We modified the regularisation coefficient values by testing values of 1, 2, 5, 8, 10 and 15 in an attempt to produce less complex and transferable models (Merow *et al.*, 2013). Models based on fine-tuned Maxent settings generally involve better discrimination ability than those based on default settings (Fan *et al.*, 2018). All the generated models were compared and selected based on the corrected Akaike information criterion (AICc) using ENMtools (Warren *et al.*, 2008).

For each training partition, 10 replicates were run (*k*-fold cross-validation) and the results averaged. Other features were set by default, with a maximum of 2000 iterations. We applied a hierarchical approach by running the models with climate variables only, then with both climate and habitat variables combined, which allows the testing of the contribution of climate and habitat features in the definition of the *C. selloana* distribution. All model performances were evaluated using AUC (area under the curve; Phillips *et al.*, 2006), TSS (True Skill Statistics) and Cohen's Kappa statistics calculated from the 10 replicates. Even though AUC is largely used, it can overestimate model performance. TSS and Cohen's Kappa provided additional perspectives on the models. A prediction no better than random gives an AUC value of 0.5, while an AUC value close to 1 indicates the highest possible model performance. The TSS ranges from −1 to 1, where 0–0.4 = poor, 0.4–0.5 = fair, 0.5–0.7 = good, 0.7–0.85 = very good, 0.85–0.9 = excellent, 0.9–1 = almost perfect to perfect. The Cohen's Kappa max statistic corrects the overall accuracy of model predictions by the accuracy expected to occur by chance and ranges from −1 to +1, where +1 indicates perfect agreement and negative values or values close to zero indicate a performance no better than random. For France, after calibration following the latter procedure, we ran models which have highest performance for each scenario A or B with either RCP 2.6, RCP 4.5, RCP 6.0 or RCP 8.5. The outputs of each model were mapped using logistic outputs with continuous probabilities ranging from 0 to 1 (Merow *et al.*, 2013). We assessed the relative contribution of each environmental and climate variable to the model using a jack-knife procedure.

Building scenario B with extra occurrences

Because we suspected that the species was undersampled in urban and suburban areas and with clear evidence of its presence, we built an additional simulated data set, named scenario B, by adding *C. selloana* occurrences to urban and suburban areas where the climate is suitable. Urban areas were based on the CORINE Land Cover 2012. We excluded all urban areas which were out of the climatic range of the species, using the same Minxent procedure described previously. Then, we identified suitable habitats (vs. unsuitable) with the maximum training sensitivity plus specificity threshold criterion (MaxTSS), which has been shown to produce highly accurate predictions (Jimenez-Valverde & Lobo, 2007), and added a *C. selloana* occurrence to each cell containing medium to low density urban areas (>75% of the cell area) or green urban areas. These added occurrences represented 361 observations. Thereafter, the same modelling approach previously described was performed.

Results

Equilibrium state in France and species climate envelopes

Invasion curves based on occurrence data did not reach a plateau at any spatial scale (Appendix S1). This indicates that the *C. selloana* invasion is probably still progressing in France. Models based only on the climate data were of good performance with AUC = 0.886 (±0.002), TSS = 0.598 (±0.020), Cohen's Kappa = 0.587 (±0.021) in South America, and 0.889 (±0.001), 0.705 (±0.011), 0.635 (±0.016) in France (Table 1). Considering climate variables, we observed discrepancies between the response curves (Fig. 2). The maximum annual temperature related to a probability of presence >0.5 ranged between 15.3 and 25.0 °C in South America and between 17.0 and 21.9 °C in France (Fig. 2A). Minimum temperatures ranged between 5.0 and 14.3 °C in the native area and between 8.7 and 14.5 °C in France (Fig. 2B). Regarding mean annual precipitations, the species mainly occurred in France where the values were 400 mm, whereas the range was larger in the native area, from 250 to 1750 mm with an optimum around 900 mm (Fig. 2C).

Contributions of climate and habitat variables

Seven environmental variables best explained the current distribution of the species in France (>1% of the total contribution; Table 2). For scenario A, minimum annual temperatures had the greatest contribution when modelled with climate data only (86.5%). When the model was run with climate and habitat variables, minimum annual temperatures and sandy areas had the greatest contribution (32.0% and 21.3% respectively). Jack-knife tests on the variables (Appendix S4) yielded the same results. With scenario B, addition of extra occurrences in urban areas logically increased the contribution of this variable at the expense of open areas, but not of climate variables that stayed stable.

Current and potential future distributions in France

Most predicted distributions (Fig. 3A,B) are concentrated around the Mediterranean basin and along the Atlantic coast, as well as inland to the east along the Loire River and to the south along the Rhône River. The map of predicted distributions for scenario B (Fig. 3C,D) indicated additional suitable sites, especially in or near large cities.

Both scenarios A and B produced good performing models for climate only and climate + habitat models (Table 1) with AUCs > 0.82, TSS > 0.58 and Cohen's Kappa max > 0.50. Modelling potential distributions with the two sets of occurrence data (A and B), and the four RCP climate change scenarios (Fig. 4), showed an overall increase in potential geographic distributions in the north and east of France for the periods 2051–2060. This increase was observed from the west coast eastwards, and along the major river corridors, Rhône valley where there are suitable climatic conditions and large urbanised areas. Most of the predicted distribution areas along the Mediterranean coast expanded northwards. Less suitable habitats persisted in all the mountainous regions like the Alps, Pyrenées, Jura, Vosges and Massif Central; nevertheless, at this scale, valleys are not visible and could contain suitable habitats.

If we consider only the suitable habitats (versus unsuitable ones), a significant increase of suitable areas (in km²) is forecasted, compared with the current distribution, from RCP 2.6 to 8.5 (+61% and +85% on average with scenarios A and B respectively). The largest area of predicted distributions was under RCP 8.5 with a mean of 322 175 km² and 481 400 km² under scenarios A and B, respectively (i.e. +69% and +116%, respectively; Table 3).

Discussion

The models with the RCP forecast a marked increase of new suitable areas for *C. selloana* for 2060. Our predictions are based on the assumption of niche

Table 1 Summary results statistics for the current distribution of *Cortaderia selloana* in France. The table shows the mean values (±SD) of the 10 replicates for both sets of occurrence data, respectively, with and without addition of occurrences in urban and suburban areas (scenarios A and B respectively)

	AUC training	AUC test	TSS	Kappa max
South America (Climate only)	0.886 ± 0.002	0.884 ± 0.023	0.598 ± 0.020	0.587 ± 0.021
France (Climate only)				
Scenario A	0.889 ± 0.001	0.884 ± 0.010	0.705 ± 0.011	0.635 ± 0.016
Scenario B	0.816 ± 0.001	0.820 ± 0.012	0.582 ± 0.014	0.495 ± 0.017
France (Climate + Habitat)				
Scenario A	0.911 ± 0.001	0.908 ± 0.009	0.717 ± 0.019	0.689 ± 0.017
Scenario B	0.866 ± 0.001	0.858 ± 0.010	0.616 ± 0.014	0.584 ± 0.014

conservatism, which remains controversial (Fernandez & Hamilton, 2015). However, *C. selloana* is still spreading in France, probably filling unoccupied suitable habitats (the climatic niche in France appears to be within in the native one).

Early and Sax (2014) pointed out that the effects of climate on species distributions, both in their native and invaded range, have been overestimated, and other non-climatic variables may be involved in range limitation, such as land use, competition or mutualistic interactions, and dispersal processes. The comparison between climate only and climate + habitat models for *C. selloana* supports this view and shows that distribution maps with habitats are more reliable and realistic. In addition, the performance of the models was improved by adding landscape and habitat variables.

Our results indicated that in France, temperature best explains the current distribution, whereas its predicted distribution will be constrained by the availability of sandy habitats, open areas with little or no vegetation and urban areas (even without the extra occurrences scenario). This is in agreement with what is known about its preferred habitats in the introduced areas, that is to say coastal habitats, riverbanks, man-made and disturbed habitats (Bossard *et al.*, 2000). The maps of suitable habitats show that major valleys may act as dispersal corridors in the future. Many sandy and disturbed habitats exist along the rivers which could be colonised by *C. selloana* (Domenech & Vila, 2006). These habitats are probably not yet all colonised because minimal temperatures may be too low. Recent studies found invasive Poaceae species like
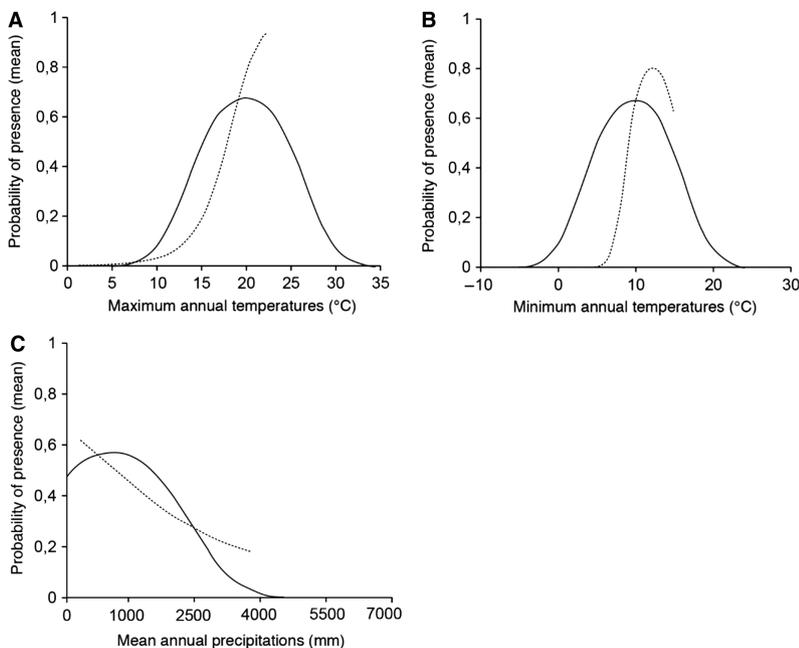
Fig. 2 Response curves (probability of presence) of the pampas grass along (A) maximal annual temperatures, (B) minimum annual temperatures and (C) annual precipitation gradients in the native area (full line) and in France (dotted line) calculated from the average monthly climate data for 1970–2000 (WorldClim v2.0). The curves show the mean response of the 10 replicated Maxent runs.

Table 2 Estimates of relative contributions of environmental variables to the explanation of the current distribution of *Cortaderia selloana* in France. The mean values are of the 10 replicated Maxent runs for both sets of occurrence data, respectively, with and without addition of occurrences in urban and suburban areas (scenarios A and B), and modelled with climate variables only and climate and habitat variables. Variables accounting for less than 1% of the total contribution are not presented

Environmental variables	Scenario A (%)		Scenario B (%)	
	Climate only	Climate + Habitat	Climate only	Climate + Habitat
Minimum annual temperatures	86.5	32.0	94.3	30.1
Sandy areas		21.3		19.3
Open spaces with little or no vegetation		21.2		9.3
Urban areas		6.2		21.9
Mean annual precipitations	4.7	6.0	3.3	7.1
Maximum annual temperatures	8.8	4.6	2.4	2.3
Forest lands		4.4		3.6
Road and railway networks		1.7		4.2
Terrestrial wetlands		1.6		1.6
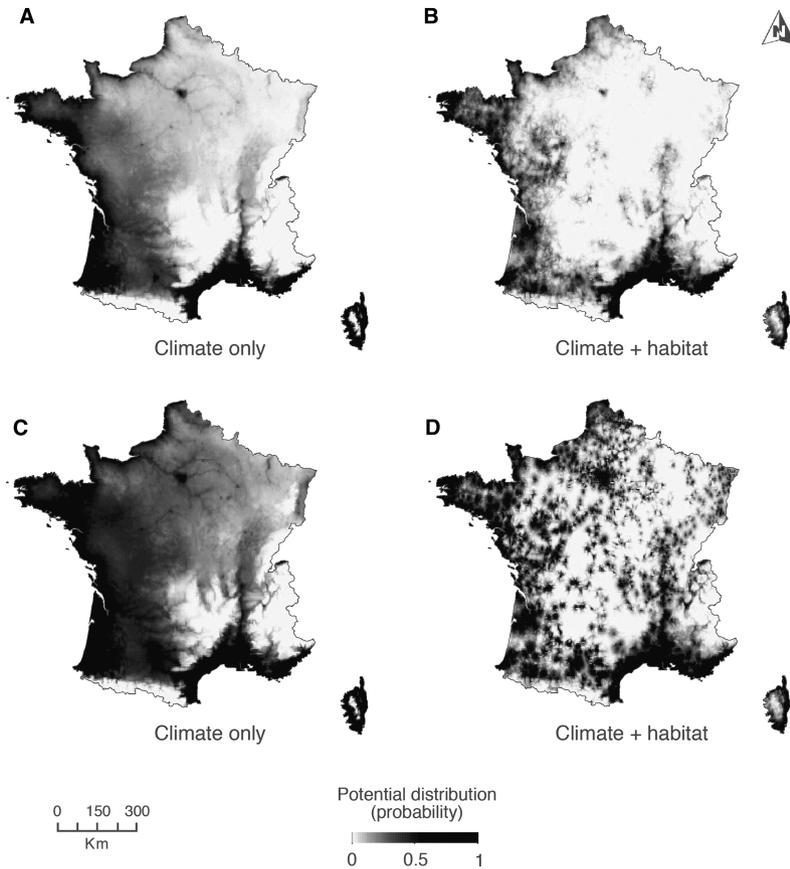
Fig. 3 Potential distribution of *Cortaderia selloana* in France under current conditions of climate only (A, C) and climate + habitat (B, D), modelled with scenario A (A and B; initial set of occurrences) and scenario B (C and D; simulated data with supplementary occurrences in urban and suburban habitats). [Colour figure can be viewed at wileyonlinelibrary.com]

Botriochloa ischaemum (L.) Keng*, Anisantha tectorum* (L.) Nevski or bamboo species to be favoured by warmer and wetter environments (Shi *et al*., 2015; Blumenthal *et al*., 2016; Takano *et al*., 2017). This trend has also been forecast with modelling approaches (Bradley, 2016). Nevertheless, *C. selloana* appears to be cold resistant, since it can be found in semicontinental climates inland and in the north of France based on the occurrences data and the models. Some isolated locations are also reported in the north of Scotland and the Netherlands.

Some climate models also predict an increase in the number, frequency and intensity of heat waves and droughts in central and southern Europe. Orsenigo *et al*. (2014) reported that these extreme climatic events may promote invasion by weeds by weakening local native species. The modelled climatic niche of *C. selloana* in its native area, and its known habitat preferences, indicates that *C. selloana* has a greater tolerance for warm temperatures and can tolerate dry conditions. The species has already weathered important drought periods in the studied introduced area, notably in southern France in 1976, 2003 and 2004.

Therefore, we hypothesise that this plant will not be greatly affected by drought events. Moreover, the species is for instance present in southern parts of South Africa, Spain and California. Since we focused on France (precise and reliable occurrence data set, good spatial resolution of habitat variables, etc.), we may have missed a part of the climatic niche which may be not covered by the native range and France. Nevertheless, France has a diversity of climate conditions on a relatively small area, which were all considered in the models and allow modelling the response of the species in the future.

When *C. selloana* occurrences were added to urban and suburban habitats (scenario B), the models predicted greater range expansion inland under the RCP scenarios. This scenario B seems more plausible than scenario A, given that invasive species are frequently used as ornamental plants in private and public gardens in suburban and urban areas. Urban and suburban areas probably act as dispersal centres under warming climate. In fact, some introduced species can have stable populations restricted to urban areas where the winter microclimate is buffered but may also
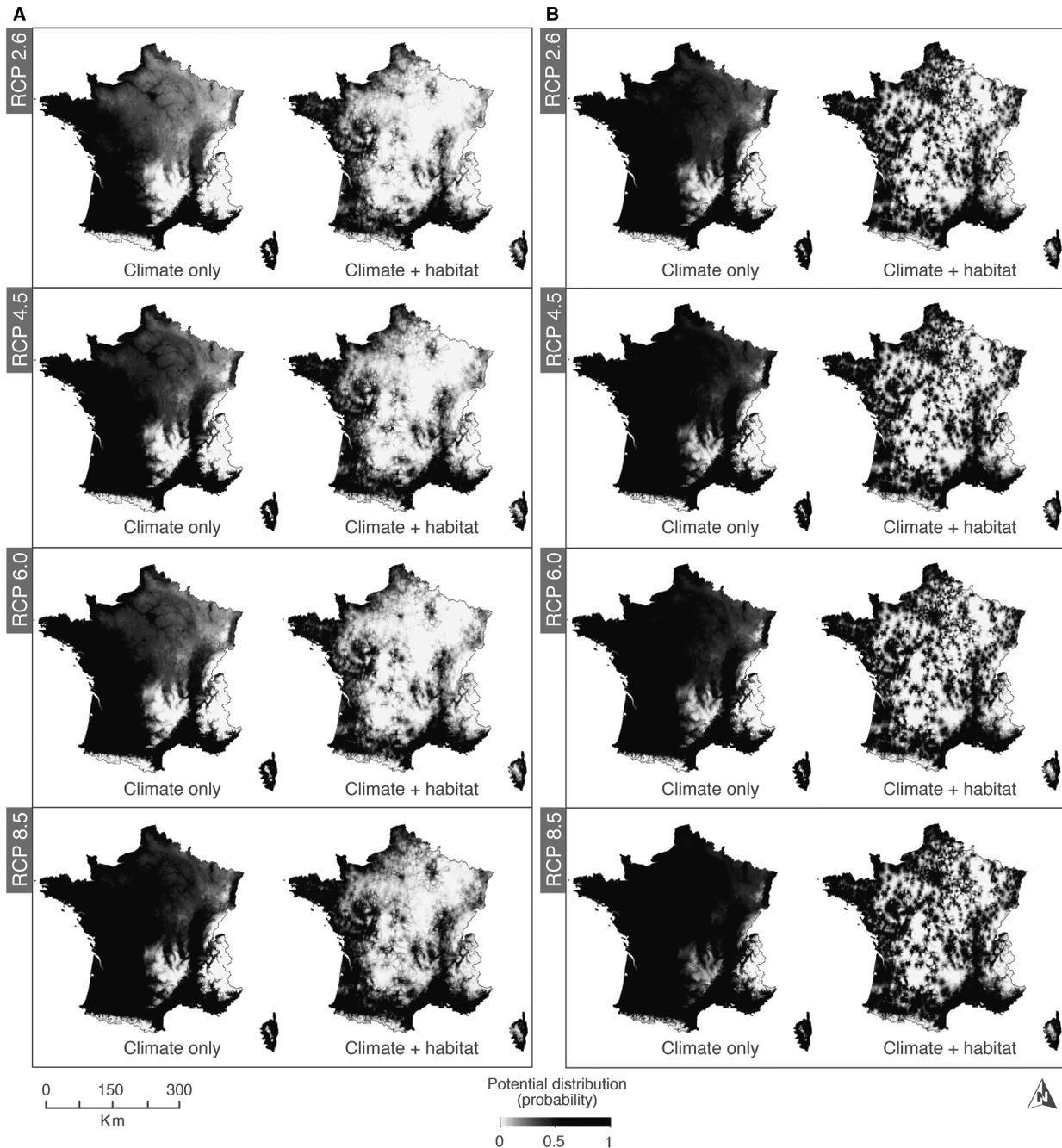
Fig. 4 Predicted distributions of *Cortaderia selloana* in France under future climate conditions (2060) with the two scenarios (A) Scenario A = presence-only data of the species and (B) Scenario B = the previous data plus additional occurrence data in urban and peri-urban areas (see *Material and methods* for details). The results were obtained based on the median of the 10 replicates of Maxent runs, selecting models with the best AUC values. [Colour figure can be viewed at wileyonlinelibrary.com]

expand their range when temperatures increase (Donaldson *et al.*, 2014). Scenario B and its associated results are in agreement with a study of an ornamental *Lonicera* species, now invasive in the United States, which showed that its current and simulated spread can be explained by the presence of suitable habitats within urban areas, coupled with high introduction rates in gardens and parks (Beans *et al.*, 2012).

Dispersal limitations were not considered in our model. Data about dispersal ability are lacking for many plant species, and integrating dispersal processes is a complex task for improving model accuracy (Miller & Holloway, 2015). Nevertheless, we believe that our distribution models are quite accurate without considering explicitly the dispersal ability of *C. selloana*, since this species produces each year a large

Table 3 Estimates of the area of suitable habitats of *Cortaderia selloana* for 2060. Results are the mean values of the 10 replicated Maxent runs for both sets of occurrence data applying the MaxTSS threshold, with and without addition of occurrences in urban and suburban areas (scenarios A and B) and modelled with climate and habitat variables. The percentage shows the difference between current and future area of suitable habitats

	Area (km²)				
	Current	RCP 2.6	RCP 4.5	RCP 6.0	RCP 8.5
Scenario A	190 225	291 300 (+53%)	304 800 (+60%)	307 800 (+62%)	322 175 (+69%)
Scenario B	222 875	355 550 (+60%)	398 775 (+79%)	471 275 (+87%)	481 400 (+116%)

quantity of light seeds easily transported by wind for 10–30 km. Consequently, its spread may be rapid and the species may easily reach suitable habitats available in the landscape. Also, Domenech (2005) concluded that, since *C. selloana* is a gynodioecious species and because functionally hermaphrodite plants act only as pollen donors, its invasive potential depends on the sex ratio of each population. Thus, the increasing populations of hermaphrodite plants in the last 25 years could have been one of the important factors in the rapid spread of the species. It has also been reported that temperature increase can interfere with seed production and release. For instance, a study by Teller *et al.* (2016) showed that seed release of wind-dispersed *Carduus nutans* was increased by temperature warming. This has not been studied for *C. selloana*, although a study found that its germination was stimulated by warmer temperatures (Bacchetta *et al.*, 2010). However, the sensitivity of the seedlings to cold may limit its invasion ability in regions where winter minimum temperatures are too low (Knowles & Ecroyd, 1985). This could explain why the most invaded zones in the world have an oceanic climate (Herrera & Campos, 2006), which is also consistent with our model results.

Implications for management

Based on the model predictions, the high ecological tolerance of *C. selloana* and the important production of wind-dispersed seeds, it is likely that the species will continue to spread across France and other European countries. *Cortaderia selloana* can be seen as a 'climate warming winner' that should also take advantage of the many urban and suburban areas where it is currently planted. Therefore, as in some European countries (Spain, for instance), its cultivation and sale must be forbidden and the species could be added to the list of invasive alien species of European Union concern pursuant to Regulation No 1143/2014 of the European Parliament and of the Council, see for instance Tanner *et al.* (2017). As for other weeds currently planted and sold in many countries, we encourage (also highlighted by Neve *et al.*, 2018) the increase in knowledge of their

occurrence/abundance, particularly for *C. selloana,* in urban and suburban areas in order to refine model predictions. As our results showed, increasing the accuracy of occurrence can lead to an increase in the modelled expansion of a species by a factor of 1.4 (according to the Table 3) depending on future climate conditions.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Equilibrium estimation in France

Appendix S2 List of habitat variables used with Maxent

Appendix S3 Collinearity among explanatory variables

Appendix S4 Jackknife tests on the variables