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► **To cite this version:**

Mathias Christina, Fawziah Limbada, Anne Atlan. Climatic niche shift of an invasive shrub (gorse, *Ulex europaeus*): a world scale comparison in native and introduced regions. *Journal of Plant Ecology*, 2019, pp.rtz041. 10.3390/d11090162. hal-02146154v1

HAL Id: hal-02146154

<https://hal.science/hal-02146154v1>

Submitted on 3 Jun 2019 (v1), last revised 15 Nov 2019 (v2)

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Climatic niche shift of an invasive shrub (*Ulex europaeus*): a world scale comparison in native and introduced regions

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ABSTRACT

Aims. Invasive species, which recently expanded, may help understand how climatic niche can shift at the time scale of the current global change. Here, we address the climatic niche shift of an invasive shrub (common gorse, *Ulex europaeus*) at the world and regional scales to assess how it could contribute to increasing invasibility.

Methods. Based on a 28,187 occurrences database, we used a combination of 9 species distribution models (SDM) to assess regional climatic niche from both the native range (Western Europe) and the introduced range in different parts of the world (North-West America, South America, North Europe, Australia and New Zealand).

Important Findings. Despite being restricted to annual mean temperature between 4 and 22 °C, as well as annual precipitation higher than 300 mm yr⁻¹, the range of bioclimatic conditions suitable for gorse was very large. Based on a native vs introduced SDM comparison, we highlighted a niche expansion in North-West America, South America and to a lesser degree in Australia, while a niche displacement was assessed in North Europe. These niche changes induced an increase in potential occupied areas by gorse by 49, 111, 202 and 283% in Australia, North Europe, North-West America and South America, respectively. On the contrary, we found no evidence of niche change in New Zealand, which present similar climatic condition that the native environment (Western Europe). This study highlights how niche expansion and displacement of gorse might increase invasibility at regional scale. The change in gorse niche toward new climatic conditions may result from adaptive plasticity or genetic evolution and may explain why it has such a high level of invasibility. Taking into account the possibility of a niche shift is crucial to improve invasive plants management and control.

Keywords Plant invasion, invasibility, niche shift, species distribution models, ecological niche

INTRODUCTION

Invasive species are challenging species distribution models, since they were introduced only recently in a new geographic area, where climatic and environmental conditions may be out of the range of those present in the area of origin. On the other hand, they provide good examples of recent species expansion that may help understand whether and how climatic niche can shift at the time scale of current global change. In addition, assessing the ecological niche of invasive species is a way of improving the efficiency of control programs by focusing on key areas whose climatic conditions are suitable under current or future climate. Increasing this efficiency is important since biological invasions are considered as one of the most serious global environmental threats (e.g. Sala *et al.* 2000; Thuiller *et al.* 2007). Plant invaders can alter the native species biodiversity and abundance modifying ecosystem processes and negatively impact human health or economic activities (Coutts-Smith and Downey 2006; Villa *et al.* 2006; Vitousek 1996;). Many countries have planned huge and costly programs to try to eliminate or control invasive species once they are established (Hill and Sandrey 1986) and the efficiency of these programs is a major issue (e.g. Andersen *et al.*, 2004). Anticipation appears the most efficient management strategy, and assessing the areas that are climatically suitable to a given invasive species is thus a key step (Leung *et al.* 2002).

At large geographical scales, climate is considered to act as the main initial coarse filter of invasive species distribution (Vicente *et al.* 2010 ; Cabra-Rivas *et al.* 2016). Niche conservatism, the tendency of species to maintain ancestral ecological requirements in native and invasive ranges (Wiens and Graham 2005), is often assumed to assess the risk of invasion (Pearman *et al.* 2008, Liu *et al.* 2017). However this assumption is still in debate nowadays for climatic niche. Evidence of climatic niche shifts have been raised for various plant invaders (Gallagher *et al.* 2010; Broennimann *et al.* 2007; Cornuault *et al.* 2015; Hernandez-Lambraño *et al.* 2016). A recent review, however, argues that niche shift can only be assessed when analog climates are compared between regions - otherwise they correspond to filling of preadapted niche - and concluded that ~85% of terrestrial plant invaders did not shift their climatic niche (Petitpierre *et al.* 2012). Webber *et al.* (2012) disagree with this argument. They consider that a species can expand its niche in two ways, either by infilling novel combinations of variables within the range present in the area of origin, or by expanding into environmental variables beyond those previously experienced. They therefore suggest that niche conservation for invasive species would be the exception rather than the rule. In any case, not taking into account climatic niche shifts of invasive population could lead to underestimate current and future biological invasions (Beaumont *et al.* 2009).

Ecological niche models (ENMs) (Guisan and Thuiller, 2005), or species distribution models (SMDs) are traditionally calibrated using native distributions and then projected onto other continents to highlight areas susceptible to invasions (Thuiller *et al.* 2005; Shah *et al.* 2012), assuming niche conservatism. Recent studies also tend to calibrate models with distribution of invaded regions, to take into account potential niche shifts and avoid underestimation of potential spread of the species. Furthermore, detecting significant deviations from niche conservatism may highlight invasive species that are characterized by

ecological (Klironomos *et al.* 2002) or evolutionary changes (Xu *et al.* 2010; Fenesi and Botta-Dukat, 2012) during invasions, helping us understand when such changes are likely to occur, which is crucial in an area of rapid climate change.

In this study, we focused on the climatic niche of *Ulex Europaeus* (common gorse), a shrub originating from Western Europe that has been introduced in many parts of the world during the 19th century. It has now been recorded in more than 50 countries and islands, and is considered as a major invasive plants, one of the 30 most noxious weed species in the world (UICN). The potential niche of gorse is considered to be unfilled and the species is still in expansion (Hill *et al.* 2008). Its geographic and climatic distribution is very wide, since it can be found at latitudes ranging from 0 to 60°N, 0 to 54°S and at altitudes ranging from sea level to 3,550 m asl (Hornoy 2012). This world-scale distribution contrasts with the relatively restricted distribution in the area of origin (from 35 to 50 °N and from 0 to 300m asl), and suggests potentially niche expansion with respect to climatic variables. Such a niche expansion of gorse was recently demonstrated by Hernandez-Lambraño *et al.* (2016) in mountain regions of South America. Here we modeled the climatic niche of gorse at a world scale, in its whole area of present distribution. This allows to compare climatic niches and its potential shift in different invaded regions.

The objectives of this study were i) To assess climatic niche of *Ulex Europaeus* at the world and regional scale based on a SDM approach, ii) to assess whether climatic niche shift occurred between native and introduced populations depending on the region and iii) to provide information for the evaluation of the degree of invasibility of introduced areas.

METHODS

Gorse presence and environmental data

Common gorse (*Ulex Europeaus*) is a highly studied invasive species, furthermore, its bright yellow flowering makes it very visible in the landscape, and it easy to identify. As a consequence, numerous data of gorse occurrence (geo-localized gorse presence) are available from various sources. Three main sources were used: online database, bibliography, and personal observations or communications (detailed in supplementary information, Table S1). In short, main online sources were from scientific network and information systems in natural sciences, biodiversity and ecology (e.g. CABI, GBIF, iNaturalist...). Bibliographic sources include scientific papers, PhD and master thesis flora, websites of local invasive species management, online reports and gray literature, amateur naturalist websites. Personal observations by our group include systematic survey in Reunion Island and Brittany, and visual observations of geolocated photos on websites such as Panoramio and Flickr. Personal communications include unpublished occurrences transmitted by professional workers on botany, ecology and nature conservation. In total, more than 100,000 records were collected. After eliminating double records, validity of the points was assessed through 3 criteria, spatial coherence (e.g. suppression of geo-localization in the sea), date of registration (only points

recorded after 1950 were retained, to be coherent with current climatic data), formal identification of the species (in case of doubt, we verified with georeferenced photos). Points corresponding to samples stocked in Herbarium or Museums were also identified and discarded. We retained 28,180 points geo-referenced around the world (see Table S2 for more details). This constitutes a quasi-exhaustive distribution of gorse at the present time. The dataset will be available in the database of the CNRS. To homogenize sample effort, we converted these geo-referenced points into a 5 arc min (10 km) grid of presence around the world. We obtained 2365 grids with gorse presence.

Data on current climatic conditions (average climate for 1950–2000; Hijmans *et al.* 2005), represented by 19 bioclimatic variables, were obtained from the WorldClim dataset (Hijmans *et al.* 2005, Table S3). We used the same spatial resolution of current climate data than for gorse presence: 5 arc min. Previous results have shown that such a broad resolution can fairly represent the climatic niche of gorse and that a finer grid did not improve the resolution of the model (Hernandez-Lambraño *et al.* 2016). To limit the set of variables used as SDM predictors and improve the accuracy of the model, we performed a Pearson correlation analysis and eliminated the most correlated variables, above a threshold of $R > 0.7$ (Barbet-Massin and Jetz, 2014). According to previous knowledge on gorse ecology, we retained 14 different combinations of 8 to 11 uncorrelated variables (Table S3).

World niche modeling and selection of the combination of climatic variables

To model species distributions at the world scale for a given climatic combination, we used nine different modeling techniques implemented within the Biomod2 package (Thuiller *et al.* 2009) in R (R Development Core Team 2017): three regression methods (GLM, MARS and GAM), a recursive partitioning method (CTA), four machine-learning methods (ANN, GBM, RF and MAXENT) and two rectilinear envelope methods (SRE, BIOCLIM). To evaluate the predictive performance of the SDMs, we used a random subset of 70% of the data to calibrate the model, and then used the remaining 30% for evaluation, using the area under the relative operating characteristic curve (AUC, Fielding and Bell, 1997). The data splitting approach was replicated five times and was the basis for calculating the mean AUC of the cross-validation. The final calibration of each model used for making projections used 100% of the available data. A current consensus distribution was obtained by calculating the weighted mean distributions across SDMs: the nine models were ranked according to their predictive performance, and a decay proportional to the evaluation score gave the relative importance of the weight.

We ran the model for the 14 different combinations of bioclimatic variables retained. The evaluation of the 14 distributions was based on AUC, sensitivity, specificity and true skill statistics (TSS; Allouche *et al.* 2006) described in Table S4. The four combinations with the best results were selected (1, 4, 7 and 9) and visually compared. After eliminating models predicting gorse presence in areas where gorse was introduced but not established (e.g. North East America), we kept the combined SDM obtained with the climatic combination n°9. It combines 9 climatic variables: annual mean temperature (Bio1), mean diurnal range (Bio2), maximum temperature of the warmest month (Bio5), minimum temperature of the coldest

month (Bio6), mean temperature of wettest quarter (Bio8), mean temperature of driest quarter (Bio9), annual precipitation (Bio12), precipitation of the wettest month (Bio13) and precipitation of the driest month (Bio14). This combination was used for all further modeling.

Regional niche modeling and projections

Based on the map of *U. Europeaus* occurrences, we selected 6 regional areas: the native area (Western Europe) and five introduced areas (North Europe, North-West America, South America, Australia and New Zealand, Fig. 1) with 672, 237, 60, 74, 1019 and 215 cell presence respectively. The case of North Europe is particular: it is not part of the natural range of distribution, but gorse was introduced there before the 19th century, and it is the only introduced area where gorse is not considered as invasive (Atlan *et al.* 2015a). First a principal component analysis (PCA) was performed on these occurrences to compare climatic data in native area and invasive areas. Kernel smooth densities were plotted for visual purpose (Fig. S1). Analyses were performed with R packages FactoMineR, factoextra and ks.

Regional SMDs were built for each area (the native and the introduced areas) following the same approach as described previously at the world scale. A first model was built using only the occurrences from Western Europe and then used to project the probability of gorse presence in introduced area (i.e. as if the species would behave like in the native area). We will refer to this model as "native model". The projections of the native model were compared with models built with the occurrence of each introduced area described previously. We will refer to these models as "introduced models". In order to transform the probabilistic consensus distribution to a presence/absence distribution, we preserved the suitability values for pixels above the sensitivity–specificity sum maximization threshold, and set the suitability for pixels under the threshold to zero (Liu *et al.* 2005; Jimenez-Valverde and Lobo, 2007, R package SDMtools). Using the simulated presence given by the models, proportion of presence depending on 4 climatic variables were calculated (Fig 3): maximum temperature (T_{MAX}) of the warmest month, minimum temperature (T_{MIN}) of the coldest month, annual precipitation (PPT) and PPT of the driest month. A PCA was performed on simulated presence to compare native and introduced climatic niche in the different introduced areas (Fig 4) following the same method as described for observed presences.

Niche change index

We used a threshold-independent niche change index to assess the difference in niche between native and introduced populations. We assess a niche overlap based on Schoener's D metric which expresses an overall fit between niches over the full environmental space and determines whether we can infer the characteristics of the introduced niche from the native niche. Based on this metric we define a global niche change index (I_{NC}) which ranges from a value of 0, where two distributions are identical, to 1, where two distributions have no overlap:

$$I_{NC} = 1 - D = \frac{1}{2} \sum_i \left| \frac{P_{INT,i}}{\sum_j P_{INT,j}} - \frac{P_{NAT,i}}{\sum_j P_{NAT,j}} \right| - 1 \quad (1)$$

where $P_{INT,i}$ is the probability of presence for *Ulex* in the cell i in the introduced model and $P_{NAT,i}$ the probability in the native model. Moreover, we quantify the potential variation in occupied area by the invasive species due to niche change:

$$I_{NC_area} = \frac{\sum_i P_{INT,i} C_{area,i} - \sum_i P_{NAT,i} C_{area,i}}{\sum_i P_{NAT,i} C_{area,i}} \quad (2)$$

where $C_{area,i}$ is the area of the cell i .

RESULTS

World scale *U. Europaeus* distribution

The world scale *U. Europaeus* (common gorse) distribution model built in this study was accurate (AUC 0.992 ± 0.002 , TSS 0.941 ± 0.01 , sensitivity 0.976 ± 0.009 and specificity 0.963 ± 0.008). The presence probability threshold calculated using the sensitivity-specificity sum maximization threshold in the model was $P = 0.48$. Only 2 % of gorse real occurrences were present in areas represented by the model below that threshold. The model predicted suitable climatic conditions in regions where gorse was effectively observed, such as Western and North Europe, North West, central and South America, South Africa, South Australia and New Zealand (Fig. 1). The model also predicted suitable climatic conditions in areas where gorse was not observed, such as East Africa or Papua New Guinea. The gorse potential distribution is globally wide and mostly along oceanic costs. At low longitude, suitable conditions were found in high altitude while in high longitude suitable conditions were found in low altitude near the costs.

World scale climatic niche

Suitable climatic conditions for *U. Europaeus* presence were wide (Fig. 2). Suitable mean annual temperatures ranged from 4 to 22°C, but the presence of gorse was limited by low temperature (below -6°C for the coldest month) and high temperature (above 32°C for the warmest month). In terms of precipitation, *U. Europaeus* was not observed when annual precipitation was below 300 mm per year. Nevertheless, it was found in environments with no precipitation over the driest month, indicating that the species can support a short period of drought.

Estimation of climatic niche shift between native and introduced areas

The geographic projections of the probabilities distribution of gorse presence, as predicted by the native model (calibrated from gorse occurrence in Western Europe) and by the introduced models (calibrated from gorse occurrences in each introduced region) will be referred hereafter as "native niche" and "introduced niche" (Fig. 3A). To compare these distributions, a kernel-smoothed PCA was performed in each introduced region, after applying the presence probability threshold (Fig. 4). The highest differences between native and introduced niches

were found in North Europe, North-West America and South America. On the contrary, native and introduced niche were similar in Australia and New Zealand. To quantify the niche differences generated by native and introduced models, a threshold-independent niche change index (I_{NC} , Fig. 4) was calculated for each introduced region ($I_{NC}=0$, where the two distributions are identical, $I_{NC}=1$, where the two distributions have no overlap, see 2.4). In agreement with the previous results, the I_{NC} for North Europe, North-West America and South America were high, 0.43, 0.47 and 0.45, respectively, while the I_{NC} for Australia and New Zealand were low, 0.20 and 0.08, respectively.

Comparison between climatic niche in native and introduced areas.

In regions with high niche change index, the introduced niches were larger (Fig. 3A) and included a larger range of climatic values (Fig. 3B) than in the native niche. In North Europe, gorse population were found in colder environments (lower temperature of the coldest month) than those predicted by the native niche. In North-West America and South America, gorse populations were found in both colder and warmer environments, particularly in regard of the warmest and coldest month. In North-West America, gorse populations were found in much drier environments than those predicted by the native niche. In regions with low change index, native and introduced niche covered similar areas, but the level of probability was higher for the introduced niche (Fig. 3A). In New Zealand, gorse populations were found in the similar range of climatic values than those predicted by the native niche. In Australia, gorse populations were found in warmer environments than those predicted by the native niche, particularly in regard of the warmest month (Fig. 3B). Accordingly, to niche change, the potential occupied area by gorse was larger when estimated by the introduced model than when estimated by the native model for all regions but New Zealand. It was larger by 49, 111, 202 and 283% in Australia, North Europe, North-West America and South America, respectively (Fig. 5).

DISCUSSION

The species distribution model built for world gorse distribution using 9 bioclimatic variables was accurate and predicted 98% of real occurrences. The potential bioclimatic niche estimated by the model was larger than the present gorse distribution, and in agreement with the assumption that the species is still expanding (Hill *et al.* 2008).

Bioclimatic conditions suitable for gorse establishment

The range of bioclimatic conditions suitable for gorse was very large. The presence of the species is restricted by annual mean temperature below 4°C and above 22°C, which corresponds to the sea level in temperate or cold regions, where it is found until 54° South and 60° North. Tropical and equatorial regions may also correspond to temperature requirements of the species, but only at high altitudes (the lower the latitude, the higher the altitude when suitable conditions can be met). The link between altitude and latitude was already observed on real distributions (Hornoy, 2011). The annual extremums. i.e. temperatures of the warmer and coldest months

are also limiting. Climates suitable for gorse are those with relatively low seasonal fluctuations of temperature, which correspond to oceanic climates. As a consequence, the species is found almost only in coastal regions, and in the North Hemisphere, on the Western sides of the continents.

Annual precipitation is more limiting, since the climatic niche excludes areas where annual precipitations are lower than 300 mm per year. However, the precipitation of the driest month is not limiting, gorse presence being possible in all the range of this variable. Delerue (2013) have shown that the seedling stage is the most sensitive to drought, which may explain why short lasting droughts are not limiting. Indeed, the fruiting season of gorse is very long (Bowman *et al.* 2008), and its seed dormancy duration highly variable (Hill *et al.* 2001; Udo *et al.* 2017), so that if the period of drought is limited in time, there is always a possibility that some seedlings emerge out of the driest period.

Solar radiation was not included in the model, but the wide range of altitude and latitude where the species can be found suggests low sensitivity to this parameter, which is confirmed by the model of Hernandez-Lambrano *et al.* (2016) for gorse in South America.

Most regions with climatic conditions corresponding to the gorse niche already contain some gorse populations. The exceptions are the central mountain chain of New Guinea, and the mountainous regions of Kenya and Ethiopia. It is difficult to know if gorse is absent from these places because it was never introduced, or because other dimensions of the niche are not met. For example, gorse cannot grow in acid soil or under forest cover (Delerue, 2013 ; Atlan *et al.* 2015b). On the other hand, these areas are difficult to access, and no colonial agriculture was developed there. Since agriculture was the main reason for introducing gorse (Atlan *et al.* 2015a), it is possible that gorse was never introduced there.

In regions where gorse is already present, it does not cover the whole range of its potential climatic niche, except in New Zealand where all favorable areas are already occupied. Gorse further expansion may be limited by other dimensions of its ecological niche, but field studies have shown that this is far from being always the case, and that the species can still expand (Hill *et al.* 2008).

Niche shift between native and invaded regions

The climatic niche estimated by the model calibrated on native or invaded regions are different. This may come from adaptive evolution in the invaded area, but also from preadaptation to conditions that are not present in the native area (Petitpierre *et al.* 2012). In this study, the Kerner-soothed analysis shows that density of probabilities of native and invasive niche are different even within the same range of parameter values. This suggests that the differences observed result at least partly from real niche shift. The niche shifts observed depended on the invasive regions considered, and almost all the situations described in the typology of Guisan *et al.* (2014) are met. This typology considers changes in the niche envelop (expansion or contraction), changes in one direction (niche displacement), and changes in the niche centroid (i.e. change in probability density). As can be deduced from Fig 4, we observe a displacement in North Europe, no significant change in New Zealand, niche expansion in South America, a combination of niche expansion, unidirectional displacement and centroid displacement in

North-West America, the same combination, at a lesser degree, in Australia, and a combination of niche expansion and multidirectional displacement in South America.

The niche expansion in South America was already shown in the study of Hernandez-Lambraño *et al.* (2016) using the model MAXENT, and is confirmed here by the combination of 9 different models. The area of presence predicted by their model is larger, probably because they consider North Europe as part of the native area, while we considered it as an introduced area. Indeed, in North Europe gorse presence results from human introduction around 1800 (Atlan *et al.* 2015a ; Udo, 2016).

Niche expansion of gorse was observed in all invaded regions but New Zealand, whose climate lies within the range of the native niche. In the other regions, the expansion of the gorse niche toward new climatic conditions may result from adaptive plasticity or genetic evolution. The species has a high potential in both. Adaptive plasticity of reproductive and vegetative traits in response to shading and resource availability was demonstrated by experimental studies and field observations (Delerue *et al.* 2013; Atlan *et al.* 2015b). Genetic evolution of life history traits was demonstrated by common garden experiments (Hornoy *et al.* 2011). Both are facilitated by the hexaploid karyotype of the species, and by its high genetic polymorphism in both native invasive populations (Hornoy *et al.* 2013).

This evolution may result from directional selection in response to different environmental conditions. They can also result from the release of natural enemies (EICA Hypothesis, Blossey and Notzold, 1995; Joshi and Vrieling, 2005). Indeed, the specific weevil *Exapion ulicis*, that can eat up to 80% of the seeds in the native region, was not introduced in the invaded regions at the same time as the plant (it was further introduced in most regions for biological control). The release from this weevil may have relaxed the genetic constraints resulting from the complex strategies of seed predation avoidance (Atlan *et al.* 2010). Following the Relaxation of Genetic Constraints hypothesis, RGC, (Hornoy *et al.* 2011), a larger level of trait combination may have contributed to niche expansion.

Consequences for gorse management and biodiversity conservation

Shift, displacement and expansion in gorse climatic niche appeared in most regions where the species was introduced. Together with its other characteristics (among which high seed production, fast growing and long survival), this may explain why it has such a high level of invasibility. The present study shows that the species has the potential to expand in many new areas, as suggested by field observation (Hill *et al.* 2008; Udo, 2016). In agricultural areas, the control of gorse is possible, providing adapted technique and financial efforts. In natural areas, its spread can be slowed by a combination of methods (physical, chemical, and biological), but its control is impossible in many circumstances. Indeed, in tropical regions, the species has a tendency to grow in altitude, i.e. in areas where the low level of anthropization often led to high levels of biodiversity and site protection, which forbid the use of unspecific methods (Hill *et al.* 2008). Early detection followed by eradication would be a means, but it is difficult to apply in scarped landscapes. In areas of the potential niche still devoid of gorse, a particular attention should be paid to avoid new introduction. In areas where gorse is already present, beyond attempts to control, the concept of novel ecosystem (Hobbs *et al.* 2006, 2009) and the study of

potential ecosystem services gorse can produce, may be a useful tools to imagine new directions of management.

The prediction of areas potentially colonized by gorse is necessary to improve the efficiency of gorse management, and to decrease its cost. These areas would have been largely underestimated without taking into account the possibility of a niche shift. The case of gorse may be an exception, as suggested by Petitpierre *et al.* (2012), but it may also be more common than previously thought, especially considering polyploid plant species. In regard of biodiversity conservation, this is a bad and good news. On the one hand, it suggests that geographic expansion of exotic species will continue beyond the climatic range of their native areas, which may threaten indigenous species. On the other hand, it shows that the capacity of some species to adapt to new climatic conditions may be higher than estimated from experimental studies, which suggest that they also have great potentialities to adapt to global climate change.

FUNDINGS

This study was financially supported by CNRS (Centre Nationale de la Recherche Scientifique), the MARIS ANR project (Agence Nationale de la Recherche, grant ANR-14-CE03-0007-01) and INRA institute (Institut National de la Recherche Agronomique).

ACKNOWLEDGEMENTS

The authors thank Morgane Barbet-Massin for her help in the modeling conception, and Michèle Tarayre and Maya Gonzalez for their helpful comments.

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FIGURES

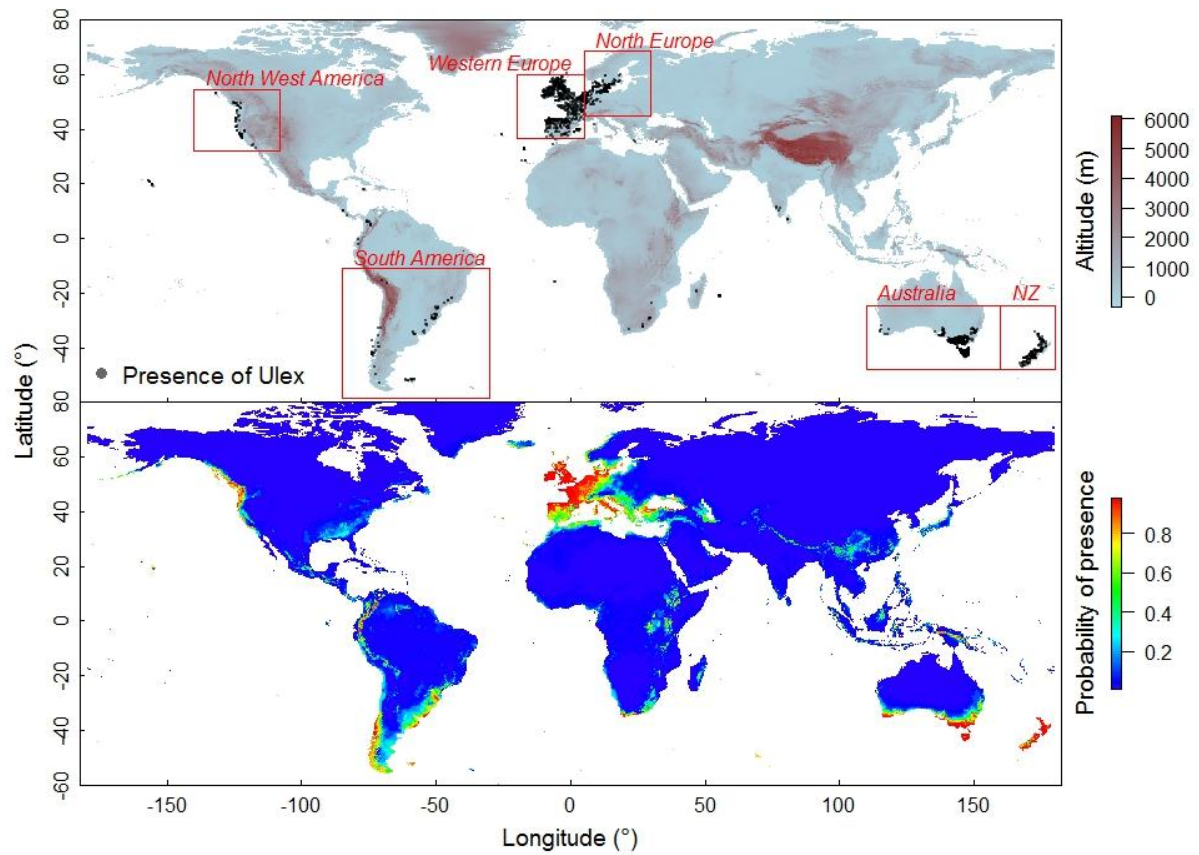


Figure 1. Current world map of *Ulex Europeanus* occurrence at the world scale (top) and probability of presence predicted by the combined species distribution model build at the world scale (below). Red squares delimit climatic areas studied to assess climatic niche shift (NZ = New Zealand).

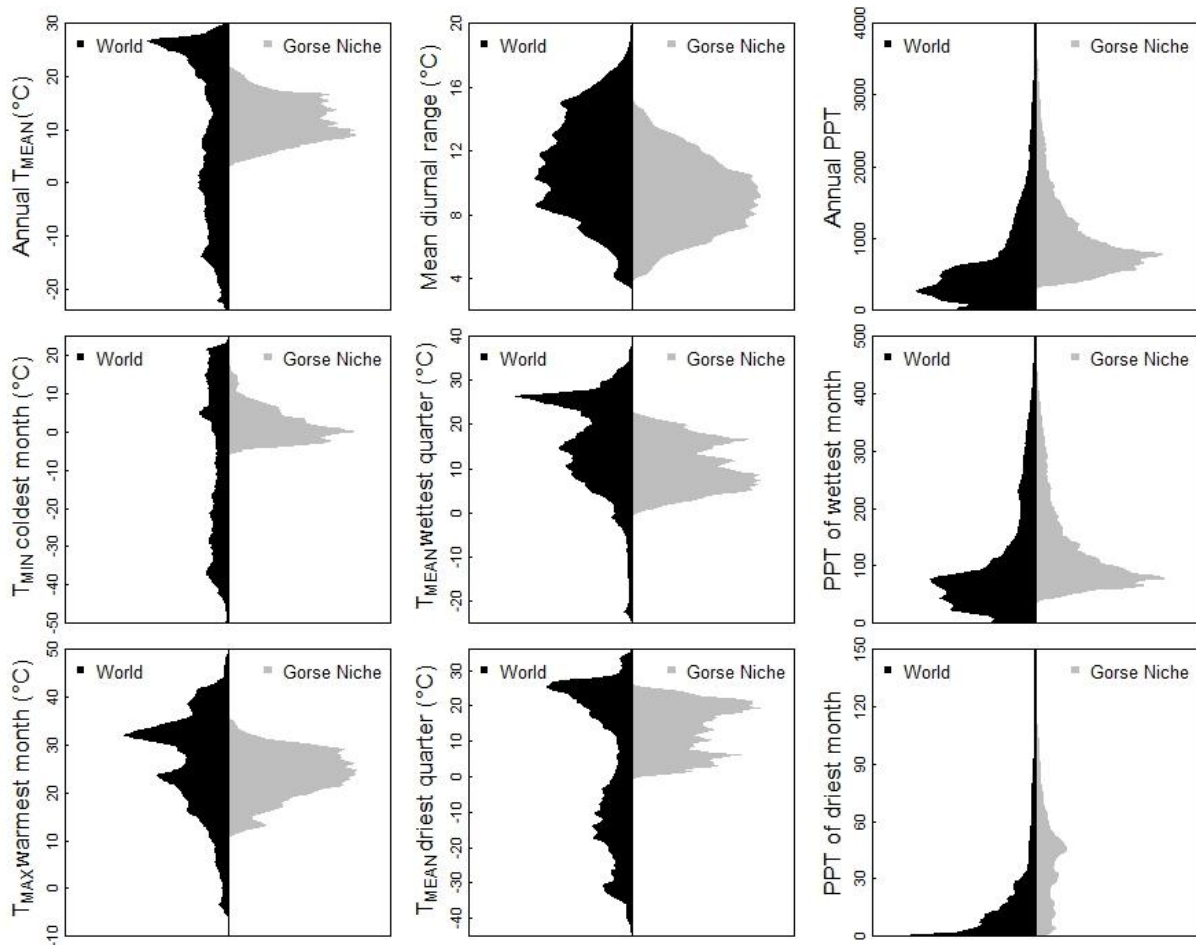


Figure 2. World scale climatic niche of *Ulex europaeus* (gorse) predicted by the combined species distribution model. The nine climatic variables used in the model are described using density distribution (beanplot R package). The world climatic variable density is presented in black while the *U. europaeus* niche is presented in gray. The presence of *U. europaeus* was assumed when its probability was higher than the sensitivity–specificity sum maximization threshold ($P=0.48$). T_{MEAN} , T_{MAX} , T_{MIN} and PPT are mean, maximum and minimum temperature, and precipitation (mm) respectively.

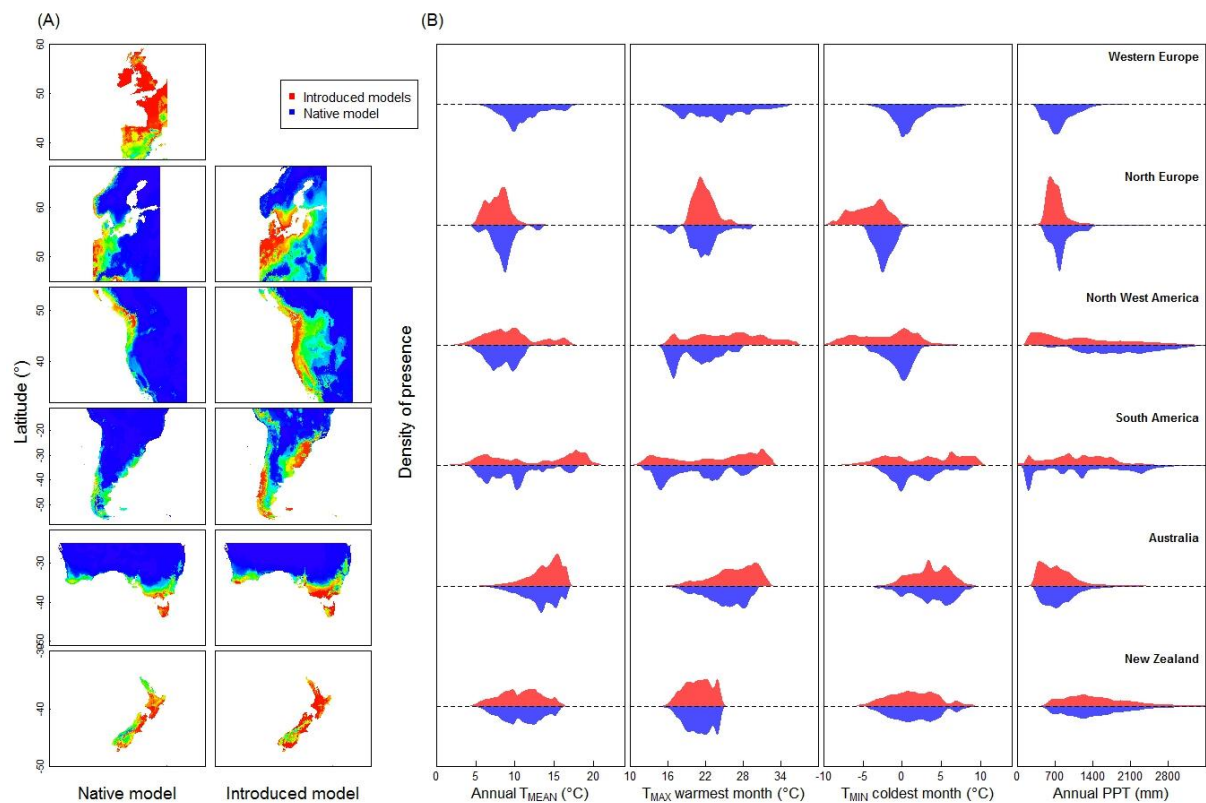


Figure 3. Probability of *Ulex europaeus* presence predicted by the native and introduced models (A). The color legend of probability is the same that the one used in Fig 1, and the area in green represents native niche for native model, and introduced niche for introduced models. Density distribution of *U. europaeus* presence (B) is presented for four climatic variables (annual T_{MEAN} , T_{MAX} of the warmest month, T_{MIN} of the coldest month and annual PPT) for both native (blue) and invasive (red) models in introduced regions, using beanplot densities. The probability of presence was converted into true presence based on the sensitivity–specificity sum maximization threshold ($P=0.48$). The vertical bars indicate the median value of the distributions.

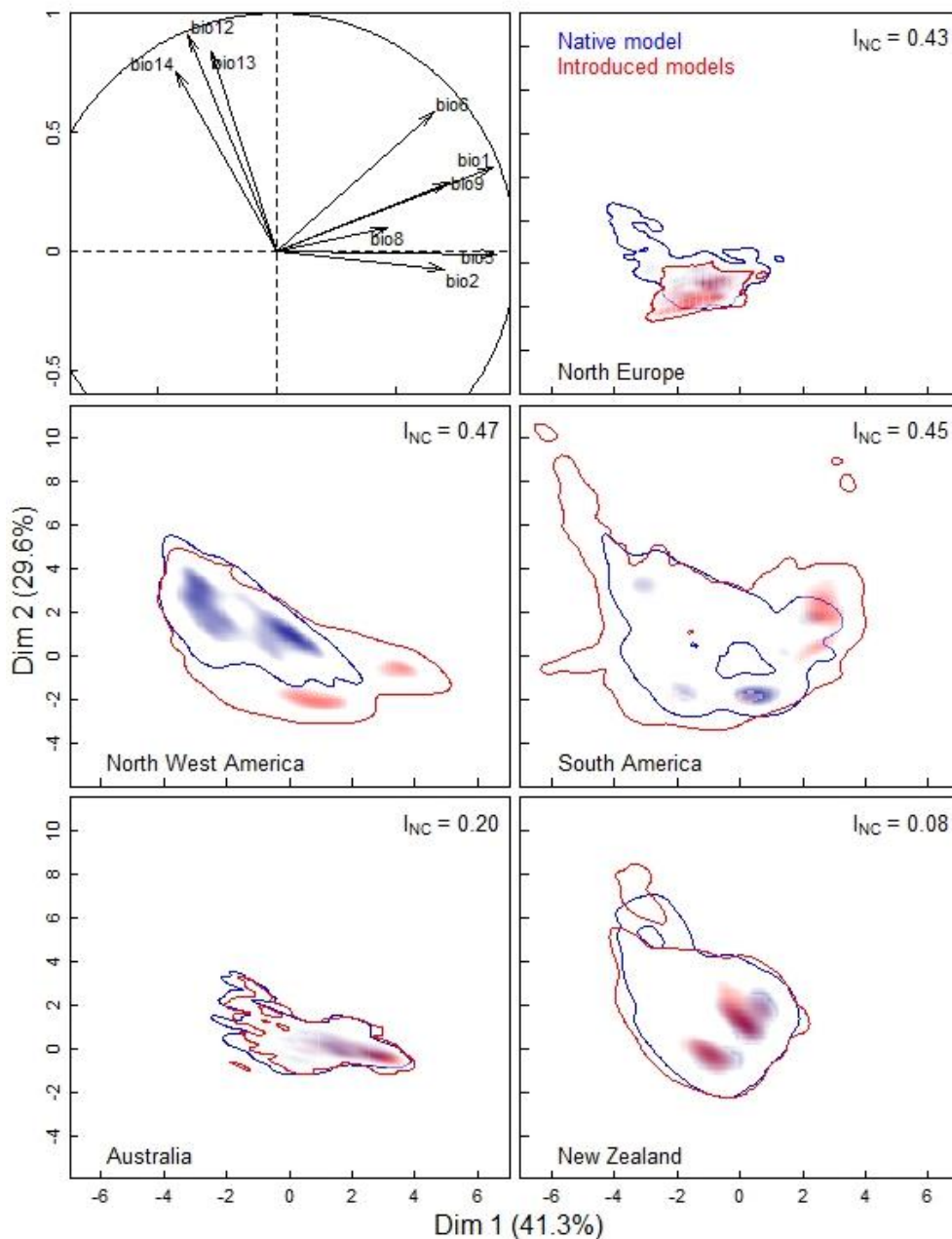


Figure 4. Comparison of native and introduced niche of *Ulex europaeus* in different introduced regions. This figure represents Kernel-smoothed PCA biplots of *U. europaeus* presence predicted by species distribution models. Correlation circles show correlations between the 9 bioclimatic variables used, with principal component axes (see M&M for variable definitions). Predicted presences were obtained after the application of a threshold on probability ($P > 0.48$). Shading indicates density of presences. The niche change index (I_{NC}) between native and introduced regions ranges from 0 (identical distributions) to 1 (no overlap).

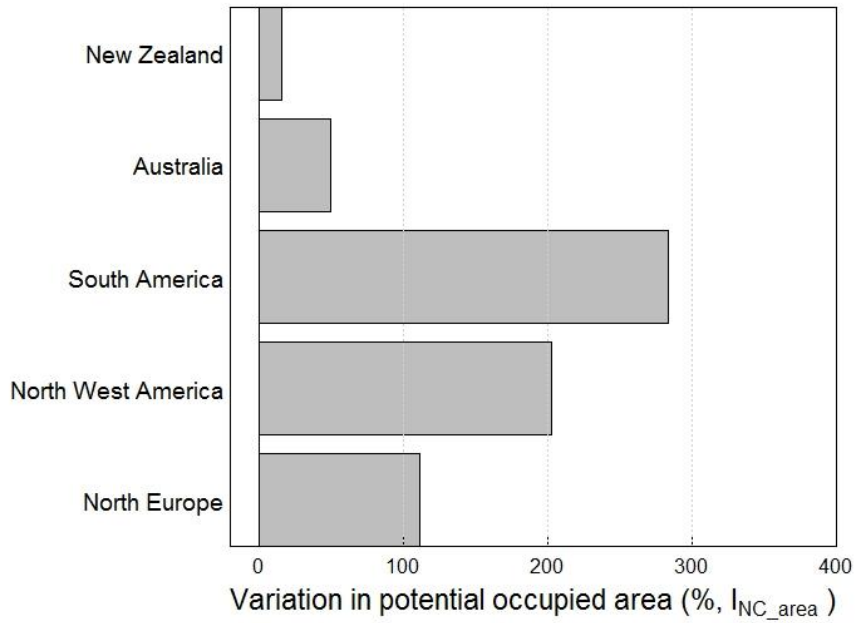


Figure 5. Variation of potential occupied areas due to niche change (I_{NC_area}) in different introduced regions. Variation is expressed by the difference between potential occupied areas predicted by the invasive model and potential occupied areas predicted by the native model. A positive value indicates an increase in area invasibility due to niche change.

SUPPLEMENTARY DATA

Table S1. Sources used to collected gorse georeferenced occurrences.

Online data repositories	Scientific bibliography	Geotagged photos	Other sources
CABI	Scientific papers	Panoramio	Invasive species management
GBIF	PhD and Master thesis	Flickr	Conservation organisms
iNaturalist	Reports	Google Earth	amateur botanists
CalFlora	Flora	Shutterstock	travel guides
Atlas of Living Australia	ILDIS	Getty Image	personal observations
Herbariums	ISSG	Alamy	personal communications

Table S2. Number of gorse georeferenced occurrences per country.

Americas	Argentina	8	Archipelagos and small islands	Azores Islands	2	Europe	Germany	97
	Bolivia	1		Ascension	1		Belgium	490
	Brazil	40		Balearic	50		Denmark	67
	Canada	12		Canary Islands	5		Spain	1068
	Chile	25		Cyprus	3		France	2627
	Colombia	12		Crete	4		Ireland	4896
	Costa Rica	6		Falklands	10		Luxemburg	14
	Ecuador	2		Hawaii Islands	28		Holland	116
	USA	102		Jamaica	2		Poland	1
	Peru	1		Madeira	30		Portugal	82
	Uruguay	3		Reunion	1005		Sweden	244
					Saint-Helena		6	United Kingdom
Africa	South Africa	18	Oceania	Australia	10994	Asia	India	4
	Algeria	1		New-Zealand	457		Sri Lanka	7
	Madagascar	2						
	Morocco	1						

Table S3. Climatic variables combinations tested in the species distribution model. For each combination, the selected variables are presented in gray.

			variable combinations													
	Designation	ID	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Temperature variable	Annual Mean Temperature	Bio_1	█	█	█	█	█	█	█	█	█	█	█	█	█	█
	Mean Diurnal Range	Bio_2	█	█	█	█	█	█	█	█	█	█	█	█	█	█
	Isothermality	Bio_3														
	Temperature Seasonality	Bio_4	█	█		█		█	█	█			█			
	Max Temperature of Warmest Month	Bio_5		█								█	█	█	█	█
	Min Temperature of Coldest Month	Bio_6			█								█	█	█	█
	Temperature Annual Range	Bio_7														
	Mean Temperature of Warmest Quarter	Bio_10														
	Mean Temperature of Coldest Quarter	Bio_11														
Precipitation variables	Annual Precipitation	Bio_12	█	█	█	█	█	█	█	█	█	█			█	█
	Precipitation of Wettest Month	Bio_13													█	
	Precipitation of Driest Month	Bio_14														█
	Precipitation Seasonality	Bio_15	█	█	█	█	█							█		█
	Precipitation of Wettest Quarter	Bio_16														
	Precipitation of Driest Quarter	Bio_17														
Mixed variables	Mean Temperature of Wettest Quarter	Bio_8	█	█	█	█	█	█	█	█	█	█	█	█	█	█
	Mean Temperature of Driest Quarter	Bio_9														
	Precipitation of Warmest Quarter	Bio_18														
	Precipitation of Coldest Quarter	Bio_19											█	█	█	█

Table S4. Accuracy results (mean \pm SD) of the 14 climatic variable combinations.

Combinations	AUC	TSS	Sensitivity	Specificity
1	0.993 (\pm 0.001)	0.944 (\pm 0.008)	0.974 (\pm 0.011)	0.968 (\pm 0.007)
2	0.989 (\pm 0.002)	0.937 (\pm 0.011)	0.982 (\pm 0.007)	0.956 (\pm 0.008)
3	0.989 (\pm 0.004)	0.933 (\pm 0.012)	0.98 (\pm 0.006)	0.953 (\pm 0.011)
4	0.99 (\pm 0.002)	0.934 (\pm 0.005)	0.981 (\pm 0.007)	0.954 (\pm 0.009)
5	0.988 (\pm 0.002)	0.922 (\pm 0.008)	0.971 (\pm 0.01)	0.951 (\pm 0.007)
6	0.989 (\pm 0.002)	0.937 (\pm 0.013)	0.98 (\pm 0.009)	0.955 (\pm 0.011)
7	0.988 (\pm 0.003)	0.94 (\pm 0.011)	0.985 (\pm 0.004)	0.954 (\pm 0.008)
8	0.989 (\pm 0.003)	0.934 (\pm 0.009)	0.981 (\pm 0.007)	0.955 (\pm 0.003)
9	0.992 (\pm 0.002)	0.941 (\pm 0.01)	0.976 (\pm 0.009)	0.963 (\pm 0.008)
10	0.987 (\pm 0.003)	0.925 (\pm 0.016)	0.977 (\pm 0.006)	0.947 (\pm 0.009)
11	0.991 (\pm 0.002)	0.934 (\pm 0.007)	0.975 (\pm 0.002)	0.959 (\pm 0.006)
12	0.989 (\pm 0.002)	0.931 (\pm 0.005)	0.974 (\pm 0.006)	0.955 (\pm 0.005)
13	0.988 (\pm 0.003)	0.925 (\pm 0.013)	0.979 (\pm 0.009)	0.948 (\pm 0.011)
14	0.989 (\pm 0.003)	0.933 (\pm 0.008)	0.976 (\pm 0.006)	0.956 (\pm 0.005)

AUC, area under the relative operating characteristic curve; TSS, true skill statistic.

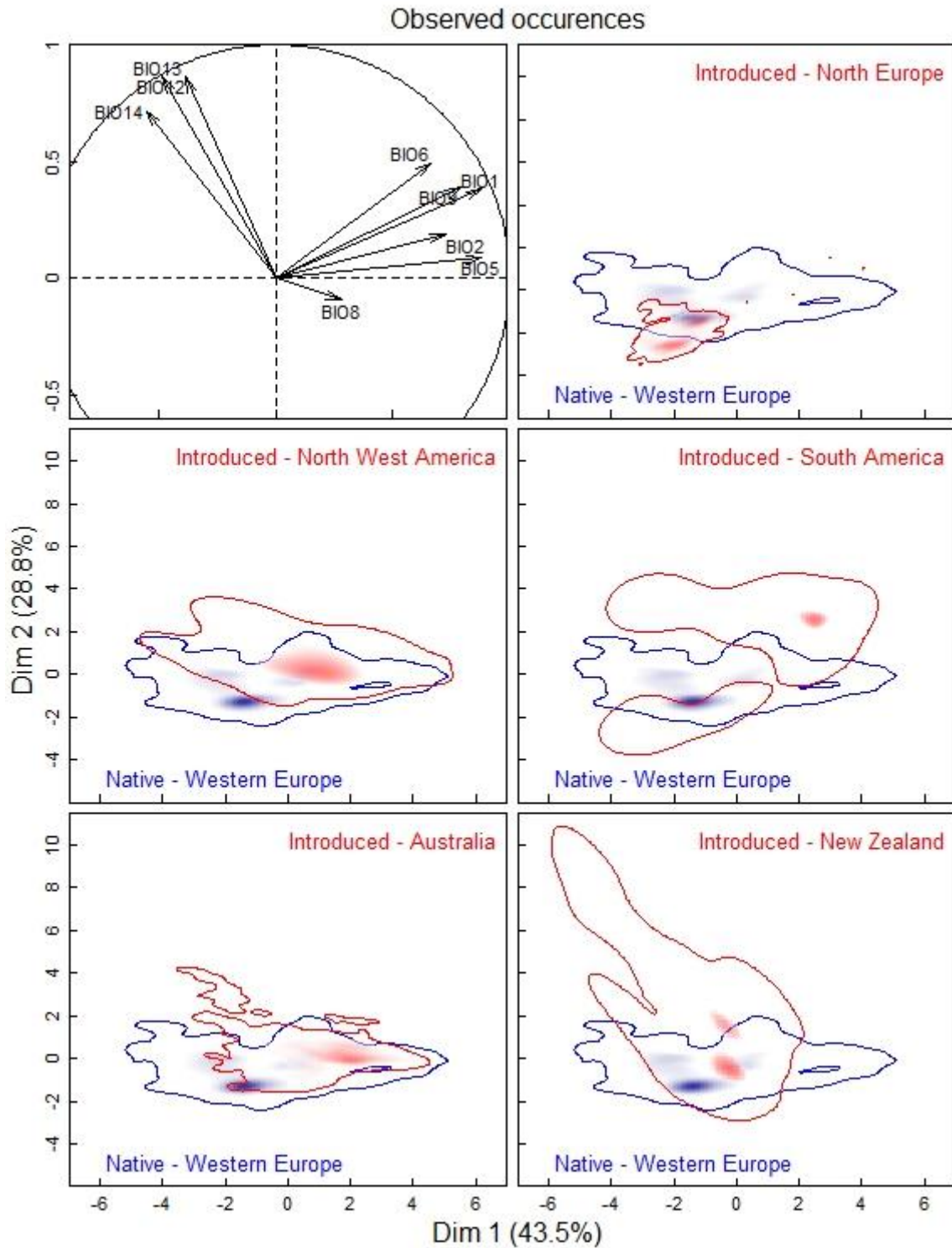


Figure S1. Kernel-smoothed PCA biplots of observed *U. Europeaus* populations, in the native area (Western Europe, blue) and different invasive area (red). Correlation circles show correlation between 9 bioclimatic variables, with principal component axes (see M&M for variables definitions). Solid lines delimit 99% of background climate. Shading indicates density of presences after kernel smoother applied.