

Evidence of climatic niche shift during biological invasion

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Abstract

Niche-based models calibrated in the native range by relating species observations to climatic variables are commonly used to predict the potential spatial extent of species' invasion. This climate matching approach relies on the assumption that invasive species conserve their climatic niche in the invaded ranges. We test this assumption by analysing the climatic niche spaces of Spotted Knapweed in western North America and Europe. We show with robust cross-continental data that a shift of the observed climatic niche occurred between native and non-native ranges, providing the first empirical evidence that an invasive species can occupy climatically distinct niche spaces following its introduction into a new area. The models fail to predict the current invaded distribution, but correctly predict areas of introduction. Climate matching is thus a useful approach to identify areas at risk of introduction and establishment of newly or not-yet-introduced neophytes, but may not predict the full extent of invasions

INTRODUCTION

Niche conservatism, the tendency of species to maintain ancestral ecological requirements (Wiens & Graham 2005), is a necessary assumption in niche-based geographical predictions of biological invasions. Under this pivotal assumption, invasion ranges can be predicted with models fitted with data from the native range (Peterson & Vieglais 2001). Anticipating future distributions of invasive species is essential for prioritization, early detection and control. Niche-based models (Guisan & Thuiller 2005) have been used to predict the invasion extents of various organisms, including beetles (e.g. Peterson & Vieglais 2001), fishes (e.g. Chen *et al.* 2007), birds and plants (e.g. Peterson & Vieglais 2001; Peterson 2003; Peterson *et al.* 2003; Thuiller *et al.* 2005). Although all of these studies assume niche conservatism in their projec-

tions, they usually do not put emphasis on quantifying possible niche shifts (e.g. percentage of divergence) as an alternative hypothesis.

Two distinct formulations of the niche conservatism concept exist that focus on either a single species or on sister taxa. In the latter multiple species situation, niche conservatism is tested by reconstructing the phylogeny of a group of related species and by testing if sister taxa are more ecologically similar than expected by random evolutionary divergence (Prinzing *et al.* 2001; Ackerly 2003; Losos *et al.* 2003). In the single species situation discussed here, niche conservatism is assessed in time or space (Martinez-Meyer *et al.* 2004) aiming to test whether a single taxon has retained similar ecological requirements across different geographical ranges or time periods.

Both niche conservatism and niche shifts can have important implications for understanding speciation, effects

of climate change and biological invasions (Wiens & Graham 2005). For instance, niche shifts are important in sympatric speciation (Losos *et al.* 2003; Levin 2005), whereas niche conservatism can explain allopatric speciation (Huntley *et al.* 1989; Peterson & Holt 2003; Wiens & Graham 2005). Niche conservatism in many species may have led to migration in response to past climate changes, and thus might drive future responses as well (Martinez-Meyer *et al.* 2004), but climate change may also create opportunities for niche differentiation and evolution, e.g. when empty niches are created at rear edges of range shifts (Ackerly 2003).

In the case of biological invasions, two factors can cause exotic species to expand beyond their predicted climate envelope in the invaded range, thus exhibiting niche differentiation between native and introduced ranges. Such niche differentiation, in effect, may result from changes in either the fundamental niche of the species (i.e. the sum of ecological situations where populations of an organism can have a positive growth; Holt *et al.* 2005), or the realized niche (i.e. the fundamental niche constrained by biotic interactions; Chase & Leibold 2003; Guisan & Thuiller 2005) or both.

First, release from biotic and abiotic constraints, such as the absence of competitors, predators or pathogens (Mitchell & Power 2003; Torchin *et al.* 2003; Callaway & Maron 2006; Mitchell *et al.* 2006) or the availability of empty niches (Hierro *et al.* 2005) may lead to a niche shift in the introduced range. These causes affect the *realized* niche of the species. Second, an exotic species may evolve in the new range allowing it to expand into new niches. Evolutionary changes can occur through genetic drift or through selection in the introduced range (Müller-Schärer *et al.* 2004; Müller-Schärer & Steinger 2004), thus affecting the *fundamental* niche of the species. Evolutionary changes can occur through genetic drift or through selection in the introduced range (Müller-Schärer *et al.* 2004; Müller-Schärer & Steinger 2004) and thus affect the *fundamental* niche of the species. Evolutionary processes may take place during and after the time lag generally observed between introduction and the spread of invasive species (Kowarik 1995; Dietz & Edwards 2006), leading to subsequent demographic and range expansion. Hence, both ecological and evolutionary changes can potentially allow a plant to shift into new habitats and climate zones, and an observed shift can equally result from a change of the realized niche, of the fundamental niche, or of both.

Empirical field evidence of climatic niche shifts during biological invasions is still lacking. Experimental studies (e.g. Sexton *et al.* 2002; DeWalt *et al.* 2004; Maron *et al.* 2004) provide some support for such processes but have limitations. For instance, growth chambers experiments (e.g. Sexton *et al.* 2002) underestimate biotic interactions

effects and their conclusions are only applicable to the fundamental niche of the species. Field studies (e.g. DeWalt *et al.* 2004) and common garden experiments (e.g. Maron *et al.* 2004) only include a very limited number of experimental sites and are most often focussing on the introduced range (Hierro *et al.* 2005). Studies investigating the realized niche of invasive species at biogeographical scales in both native and non-native ranges are necessary to quantify niche shifts accurately (Hierro *et al.* 2005). Reciprocal geographic predictability between the two ranges is one approach that has been suggested (Wiens & Graham 2005).

We conducted a large biogeographical study on the herbaceous spotted knapweed *Centaurea maculosa* L. This is an excellent species for testing the hypothesis of niche shift associated with biological invasions. It was first introduced in the 1890s from Europe into western North America, where it now infests over 3×10^6 ha of rangeland and pasture in 14 states and two Canadian provinces (Story *et al.* 2006) and may cause an estimated $>150 \times 10^6$ US\$ in economic damage each year (Story 2002). In both ranges, the species occurs in disturbed and natural grassland habitats, but it rarely reaches densities in the native range as high as observed in the invaded range (Müller 1989). The species has not undergone any artificial selection nor hybridization to improve ornamental traits, which ensures that an observed niche shift is likely to result from natural processes.

We examined the climatic niche of *C. maculosa* in its native and invaded ranges to test whether the species exhibits niche conservatism, a pivotal assumption for enabling reciprocal geographic predictability between the two ranges. We used comprehensive occurrence data from all regions where the species is present in Europe and western North America, fully covering the relevant large climatic gradients and eliminating risk of fitting truncated response curves and thus only partially fitting models to the species' realized niche (Thuiller *et al.* 2004). The niche we define here thus reflects all climatic conditions where the plant can survive and reproduce in the presence of biotic interactions. We are not aware of comparably robust data for any other invasive species across two ranges.

MATERIALS AND METHODS

Species occurrence data collection

We collected all occurrences available for *Centaurea maculosa* Lam. (syn *C. stoebe* L.) in Europe and western North America. The taxonomic treatment of *C. maculosa* is unclear (Ochsmann 2000, Flora Europaea database 2007; <http://rbg-web2.rbge.org.uk/FE/fe.htm>). Therefore, we considered *C. maculosa* s.l. as the taxonomic entity. Two subspecies

have been suggested for the species, associated with its two ploidy levels: *C. stoebe* L. subsp. *stoebe* (diploid) and *C. stoebe* L. subsp. *micranthos* (Gugler) Hayek (tetraploid; Ochsmann 2001). Although it was hypothesized that the species' distribution was restricted to south-central and south-east Europe at the time of introduction to North-America (Ochsmann 2001), models fitted based on a more restricted native range would result in a larger niche shift, making our approach conservative. The same applies for a more narrow taxonomic treatment.

Occurrences for Europe were acquired through herbarium data and completed by several field surveys done by the two first authors during summer 2005. For western North America, occurrences were obtained through different land management and state agencies. Only occurrences with locational accuracy equal to or finer than the resolution of climate data were kept. The final database consisted of 275 occurrences for Europe and 1685 for western North America.

Climate data

We used global climatic data sets used in previous studies of plant distributions (Guisan & Thuiller 2005; Thuiller *et al.* 2005) that have been recommended for cross-continental tests of niche conservatism (Wiens & Graham 2005). As the choice of climatic data may influence the result, we performed separate series of analyses based on three existing global coverage climate maps, CRU 0.5° (New *et al.* 1999), CRU 10' (New *et al.* 2000) and WORLDCLIM (Hijmans *et al.* 2005) (Table 1). As these sets of maps were independently prepared at three different resolutions (10' and 0.5° and 1 km respectively), we ensured the replicability and reliability of the analyses.

The 19 original WORLDCLIM bioclimatic variables were used without modifications. From the original CRU 10' base maps we derived a data set containing eight bioclimatic variables commonly used in other studies. A data set of five coarser annual variables from CRU 0.5° was also tested (Table 1).

Testing for climatic niche conservatism

Principal component analysis (PCA) was run to compare the position of occurrences from the native and invaded range in the climatic space, using the 'ade4' library in the R software. Occurrences were weighted to ensure an equal representation of the two ranges in the analyses. The magnitude and statistical significance of the niche shift between the two occurrence clouds in the PCA graph were assessed using a between-class analysis, yielding a between-class inertia percentage (Dolédéc & Chessel 1987). We further tested this ratio with 99 Monte-Carlo randomiza-

Table 1 List of predictors available in each climatic data set

Data set	Variable	Description
WORLDCLIM	BIO1	Annual mean temperature
	BIO2	Mean diurnal range
	BIO3	Isothermality
	BIO4	Temperature seasonality
	BIO5	Max temperature of warmest month
	BIO6	Min temperature of coldest month
	BIO7	Temperature annual range
	BIO8	Mean temperature of wettest quarter
	BIO9	Mean temperature of driest quarter
	BIO10	Mean temperature of warmest quarter
	BIO11	Mean temperature of coldest quarter
	BIO12	Annual precipitation
	BIO13	Precipitation of wettest month
	BIO14	Precipitation of driest month
	BIO15	Precipitation seasonality
	BIO16	Precipitation of wettest quarter
	BIO17	Precipitation of driest quarter
	BIO18	Precipitation of warmest quarter
	BIO19	Precipitation of coldest quarter
CRU 10'	aet/pet	Ratio of actual to potential evapotranspiration
	pet	Potential evapotranspiration
	prec	Annual amount of precipitations
	std_prec	Annual variation of precipitations
	tmin	Minimum temperature of the coldest month
	tmax	Maximum temperature of the warmest month
CRU 0.5°	gdd	Growing degree-days above 5 °C
	tmin	Minimum temperature of the coldest month
	tmax	Maximum temperature of the warmest month
	rad	Annual amount of radiations
	prec	Annual amount of precipitations

tions (Romesburg 1985). To locate the climatic position of the species inside European and Western North American climates, we projected all pixels of study areas in the same PCA climatic space.

Fitting niche-based species distribution models

It has been recently shown that different modelling techniques calibrated on the same species can produce different results (Thuiller 2004; Araujo *et al.* 2005). As recently suggested, we use a combination of these techniques to adjust for the inherent uncertainty from these models and to find the optimal solution from an ensemble of predictions (Thuiller 2004; Araujo & New 2007).

For such a purpose, we used the latest release of the BIOMOD tool (Thuiller 2003) implemented into the R software (R Development Core Team 2005), including four additional techniques. The following eight techniques were used for our reciprocal modelling analyses: artificial neural networks (ANN), boosted regression trees (BRT), classification tree analyses (CTA), generalized linear models (GLM), generalized additive models (GAM), multivariate adaptive regression splines (MARS), mixture discriminant analysis (MDA) and random forests (RF). GLM, GAM, CTA and ANN are described and discussed in the original BIOMOD paper (Thuiller 2003). BRT and MARS were recently tested, together with GLM, GAM and CTA in a large study comparing 16 predictive techniques (Elith *et al.* 2006), BRT ranking best. MDA (Hastie & Tibshirani 1996) and RF (Breiman 2001) were also added as promising modelling methods. As only occurrences were available, pseudo-absences were generated (Graham *et al.* 2004) to fill the absence component of the models. Following recent recommendations (Elith *et al.* 2006), this was done randomly. The procedure was repeated 100 times with each technique, using a different set of calibrating presences and absences within each iteration to ensure robustness of the predictions and provide uncertainty estimates (Fig. 2).

Model evaluation

We tested the predictive power of each model in the range where it was calibrated, using an independent data set (30% of the total), as well as in the range where it was projected, by comparing model predictions to real observations, using the area under the curve (AUC) of a receiver-operating characteristics (ROC) plot (Fielding & Bell 1997; Elith *et al.* 2006). The AUC allowed testing of whether the pattern predicted in the other range differed significantly from a random prediction, compared to the prediction achieved in the same range. Following Swets' scale (Swets 1988), predictions are considered random when they do not differ from 0.5, poor when they are in the range 0.5–0.7, and useful in the range 0.7–0.9. Predictions greater than 0.9 are considered good to excellent (1 = perfect). AUC values under 0.5 reflect counter predictions (omission and commission rates higher than correct predictions).

RESULTS

The analyses provided the same results and supported the same conclusions whatever the climatic data set used. Only the results conducted with the eight CRU 10' climatic maps are presented here, because (1) these were considered biologically more relevant for the species (Guisan & Thuiller 2005) and (2) they constitute the baseline data set used by the Intergovernmental Panel for

Climate Change and were already used in similar studies (Thuiller *et al.* 2005). The eight CRU 10' climatic maps were: ratio of actual to potential evapotranspiration (aet/pet), potential evapotranspiration (pet), annual amount of precipitations (prec), annual variation of precipitations (std_prec), minimum temperature of the coldest month (tmin), annual mean temperature (tmp), maximum temperature of the warmest month (tmax) and growing degree-days above 5 °C (gdd). Results obtained with other climatic data sets are available in the Supplementary Material.

Principal component analysis of the pooled climatic data revealed two significant axes of climatic variation, defining a realized climate space of reduced dimensionality which allows the investigation of niche conservatism (Fig. 1). The enclosed correlation circle (Fig. 1, see also Table 2) indicates the relative contributions of climatic predictor variables to axis 1 and 2. The two axes are associated closely with water availability and heat energy, respectively. Examination of the position of the species in climate space reveals that niche centroids differ strongly between the native and introduced ranges of the species (between group inertia: 31.8%; $P < 0.01$), in spite of extensive overlap of European and western North American climates (Fig. 1). The niche shift occurs principally along axis 1, indicating water availability as the underlying gradient of niche differentiation. Supporting this idea, spotted knapweed in North America is known to be highly efficient at capturing available moisture, allowing it to exploit drier sites (Story 2002).

Reciprocal prediction of the species' distribution between the two ranges further confirmed this niche shift. If realized niches were conserved, models fitted in the native range would predict the extent of potential invasion in the new range (Wiens & Graham 2005). However, models of *C. maculosa* fitted in Europe failed to predict the western North American distribution and vice versa, independent of modelling technique and climatic data set (Fig. 2). To avoid methodological artefacts, we derived geographical predictions using eight different modelling techniques, and subsequently fitted each model 100 times with resampled data to quantify uncertainties in predictions (Fig. 2). Interestingly, fitting models at coarser resolution with annual climatic parameters not accounting for seasonal variability somehow reduced the divergence of predictions between the two ranges (AUC increased 7.9% in average among the eight modelling techniques using CRU0.5 data set; see Supplementary Material), hypothesizing either that niche differentiation may occur more in the seasonally relevant climatic variables than in coarse climatic features or that the 'bioclimatic' parameters may be overspecifying niche models, reducing their generality.

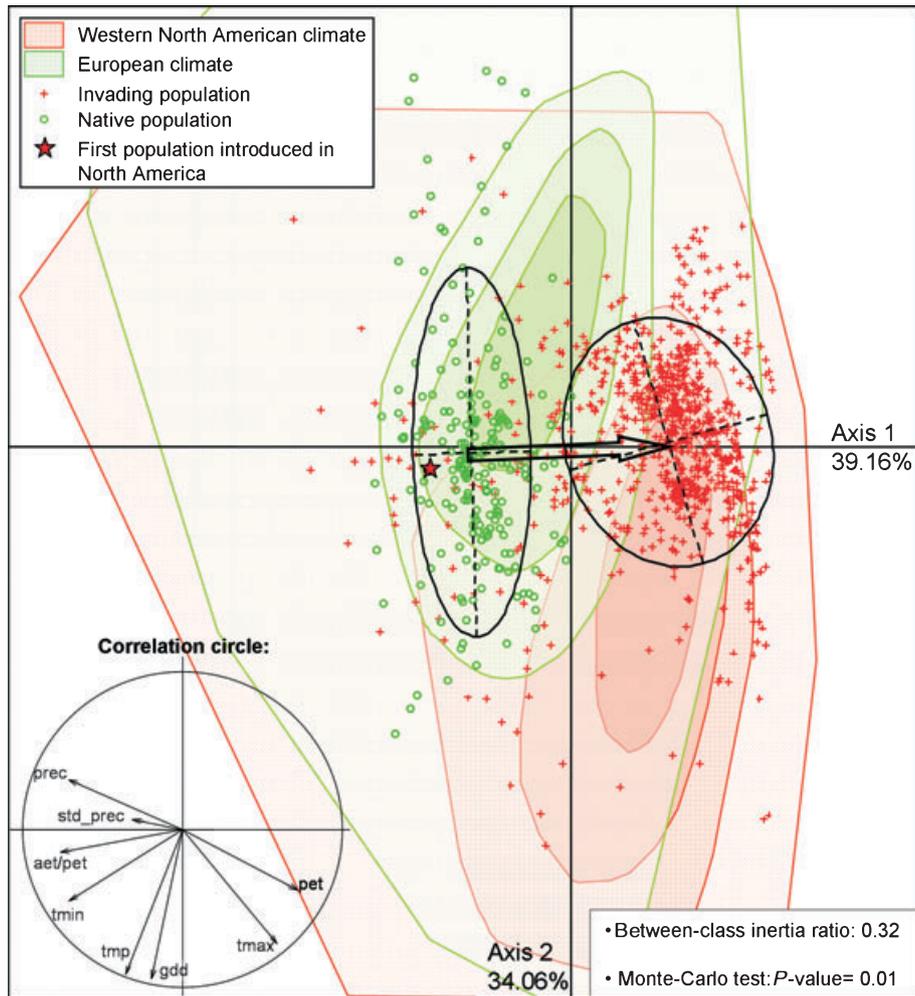


Figure 1 Bioclimatic space with illustration of niche shift. The position of occurrences, from the native and invaded ranges along the principal climatic gradients is indicated with green dots and red crosses respectively. The red star shows the climatic position of the first population introduced in North America (Victoria, BC). The arrow linking the centroids of the 1.5 inertia ellipses for the two ranges illustrates the niche shift. The enclosed correlation circle indicates the importance of each bioclimatic variable on the two significant axes of the principal component analysis (PCA), which jointly explain 73.22% of the variance in the data. A between-class analysis, yielding a between-class inertia ratio, was further conducted and tested with 99 Monte-Carlo randomizations. The convex hulls indicate the prevalence (25, 50, 75 and 100% of sites included) of the global climate conditions in the two ranges. Climatic predictors are: tmp = annual mean temperature, tmax = maximum temperature of the warmest month, tmin = minimum temperature of the coldest month, prec = annual sum of precipitation, std_prec = annual variation of precipitation, gdd = annual growing-degree days above 5 °C, aet/pet = ratio of actual to potential evapotranspiration, pet = annual potential evapotranspiration.

DISCUSSION

Our results clearly suggest a climatic niche shift of Spotted Knapweed during or subsequent to invasion of this species. The study was based on a comprehensive occurrence data from all regions where the species is present in Europe and western North America, fully covering the relevant climatic gradients. Although distribution data of exotic species are increasingly available within their introduced ranges, obtaining similar data from the native range often remains difficult (Peterson *et al.*

2003). We put particular effort in acquiring data from the native species range by performing our own field sampling. We are not aware of comparably robust data for other invasive species across two ranges.

These results have important implications for studies of biological invasions, as they provide the first empirical field evidence of such phenomenon. The distribution of invading and native population along climatic gradients (Fig. 1) shows that none of the native populations grows in a similar climate as the vast majority of the invading populations in western North America. However, some of the invading

Table 2 Weighting of each climatic variable in the PCA analyses. Values indicate the relative contributions of climatic variables to axis 1 and 2. Values ranging between [0; 1] indicate a positive contribution to the axis, while values ranging between [-1; 1] indicate a negative contribution.

Climatic variable	Influence on axis 1	Influence on axis 2
aet/pet	-0.464	-0.087
gdd	-0.118	-0.572
pet	0.434	-0.232
prec	-0.432	0.192
std_prec	-0.191	0.039
tmax	0.356	-0.436
tmin	-0.431	-0.273
tmp	-0.217	-0.555

populations still grow under similar climatic conditions as the native populations, and thus have conserved their climatic niche. As none of the native populations can be found in the

climatic core area of the invasion, the niche shift we illustrate here occurred in the invading range. Thus, it does not seem related to a specific subgroup of native populations.

In this study, the observed niche reflects the realized niche of the species, including effects of interactions with other species. Thus, the observed niche shift could result either from changes in the species' fundamental niche, as caused by an evolutionary process (e.g. hybridization or evolution of increased competitive ability; Blossey & Notzold 1995) or from changes in the realized niche, as caused by a different biotic environment in the introduced range (e.g. enemy-release hypothesis; Keane & Crawley 2002), or from both (Dietz & Edwards 2006).

From an ecological perspective, some climatic factors may be only indirectly related to the shift, and other more proximal non-climatic factors may have played a more prominent role. Shifts in other dimensions of the niche, such as soil types, could also be investigated in a similar way. In the new range, Spotted Knapweed has been shown to

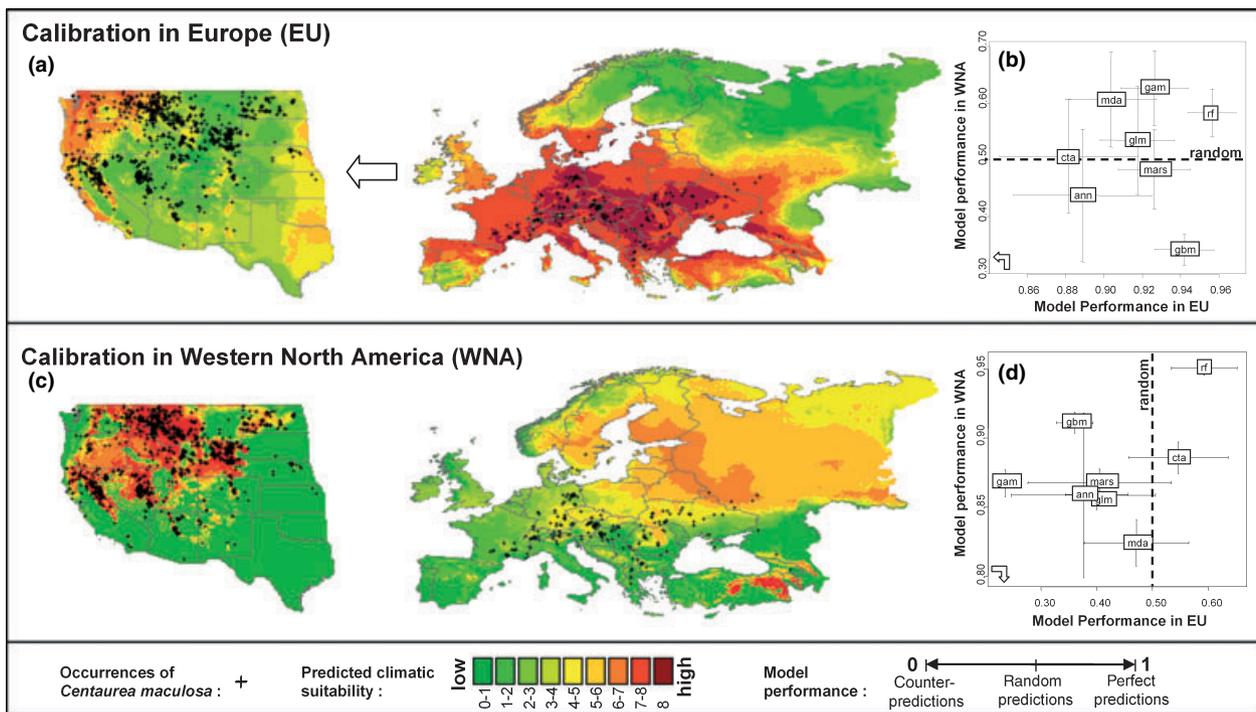


Figure 2 Prediction maps and model evaluation. The upper and lower boxes illustrate, respectively, the results obtained from models calibrated in Europe (EU; a, b) and Western North America (WNA; c, d), and projected into the other range. The maps (a, c) show the predicted climatic suitability (mean number of models, among eight modelling techniques, predicting the species present). The series of graphs (b, d) plot model performance [area under the curve (AUC)] for 100 repetitions of each technique, based on random re-sampling of the data. The AUC (see Supplementary Material) of a receiver-operating characteristic (ROC) curve calculated on independent data is currently the most objective measure of model performance for presence-absence data, with 1 indicating perfect prediction, 0.5 not different than random and 0 a perfect counter prediction. The horizontal axis indicates the model performance of the predictions in the native area (EU). The vertical axis indicates the model performance of the predictions in the invaded area (WNA). The horizontal and vertical dashed lines indicate predictions that do not differ from random (AUC = 0.5) when projected in the other area (WNA in b; EU in d). Error bars indicate the standard deviation of each modelling technique for the 100 repetitions. As (b) and (d) show, both reciprocal predictions fail, with AUC values centred on 0.6 for the best technique, but for most others being not significantly different from 0.5 or below (counter-predictions).

benefit from biotic release from competitive neighbours through novel weapons (Callaway *et al.* 2004, but see Blair *et al.* 2005, 2006), from soil pathogens (Callaway & Maron 2006; Hierro *et al.* 2006) and from escaping specialist root herbivore insects that dominate the complex of natural enemies in the native range (Story *et al.* 2006). However, in the latter biocontrol study, the insects can be abundant in very dense stands of knapweed, indicating that the plant may overcome the damages done by the insects in particular ecological situations. These three processes may have promoted niche shifts into climatic conditions from which the species was naturally excluded in its native range.

From an evolutionary perspective, the fact that the niche determinants may differ between native and invaded ranges is supported by experimental studies suggesting rapid evolution of invasive plants (Sexton *et al.* 2002; DeWalt *et al.* 2004; Maron *et al.* 2004). It was also hypothesized that both diploids and tetraploids of *C. maculosa* were introduced from the native range, but only tetraploids became invasive (Müller-Schärer *et al.* 2004). The observed niche shift may thus be solely associated with a shift in the frequency of ploidy levels. However, the fact that none of the native populations has climatic requirements similar to those observed in the climatic core area of the invasion (Fig. 1) refutes this hypothesis. This was further confirmed by a ploidy analysis showing a similarly large climatic shift between the European and North-American tetraploid populations (Treier, *et al.*, unpublished results).

Given that gene flow between the two ranges is low or absent, likely factors influencing niche evolution include time since invasion in which evolutionary processes can have occurred, and the magnitude of environmental (climatic or biotic) differences. Evolutionary niche shift may therefore only be quantifiable for species present for sufficient time in the new range (> 120 years for *C. maculosa*). As supporting evidence, the first accidental introduction of *C. maculosa* was in Victoria, BC (Roche *et al.* 1986), a place predicted as highly suitable by the European models (Figs 1 and 2a).

The invaders database (<http://invader.dbs.umt.edu>) provides a chronological description of the species spread in north-western USA. A first specimen was recorded in Ravalli, Montana, in 1920. The high number of records done in drier habitats in Montana and north-western America during the succeeding years seems to indicate that the date of introduction of the plant there occurred approximately at the same period, 30 years after its introduction in Victoria, BC. This is, to our knowledge, the only documented chronology of introduction available for this plant. Multiple, possibly simultaneous, introductions could have occurred, but only phylogenetic studies can answer this question.

Our results have particularly important implications for application of niche-based species distribution models to

predict future areas prone to invasions (Peterson & Vieglais 2001; Thuiller *et al.* 2005). Our results report, for the first time, a climatic niche shift during biological invasion, and thus support the hypothesis that species can spread into new habitats never been used before by the species (Dietz & Edwards 2006). In particular, this means that an invasive species can occupy new niches that are not predictable from knowledge of the native range alone, calling for more cautionary interpretation of model predictions. Nonetheless, the areas where the species was first introduced proved to be correctly predicted by models. Therefore, the approach of using niche-based models to predict the spread of potential invaders into new areas (Peterson 2003; Thuiller *et al.* 2005) is still useful to identify areas at risk of successful introduction and establishment of newly or not-yet-introduced neophytes. However, it may not predict the full invasion potential in the new range.

As a further step, our results could provide a framework to design more local and proximal studies of niche shifts, for instance by investigating shifts along biotic factors or identifying other more mechanistic processes behind such climatic niche shifts, at contrasted climatic sites as revealed by predicted species distribution maps.

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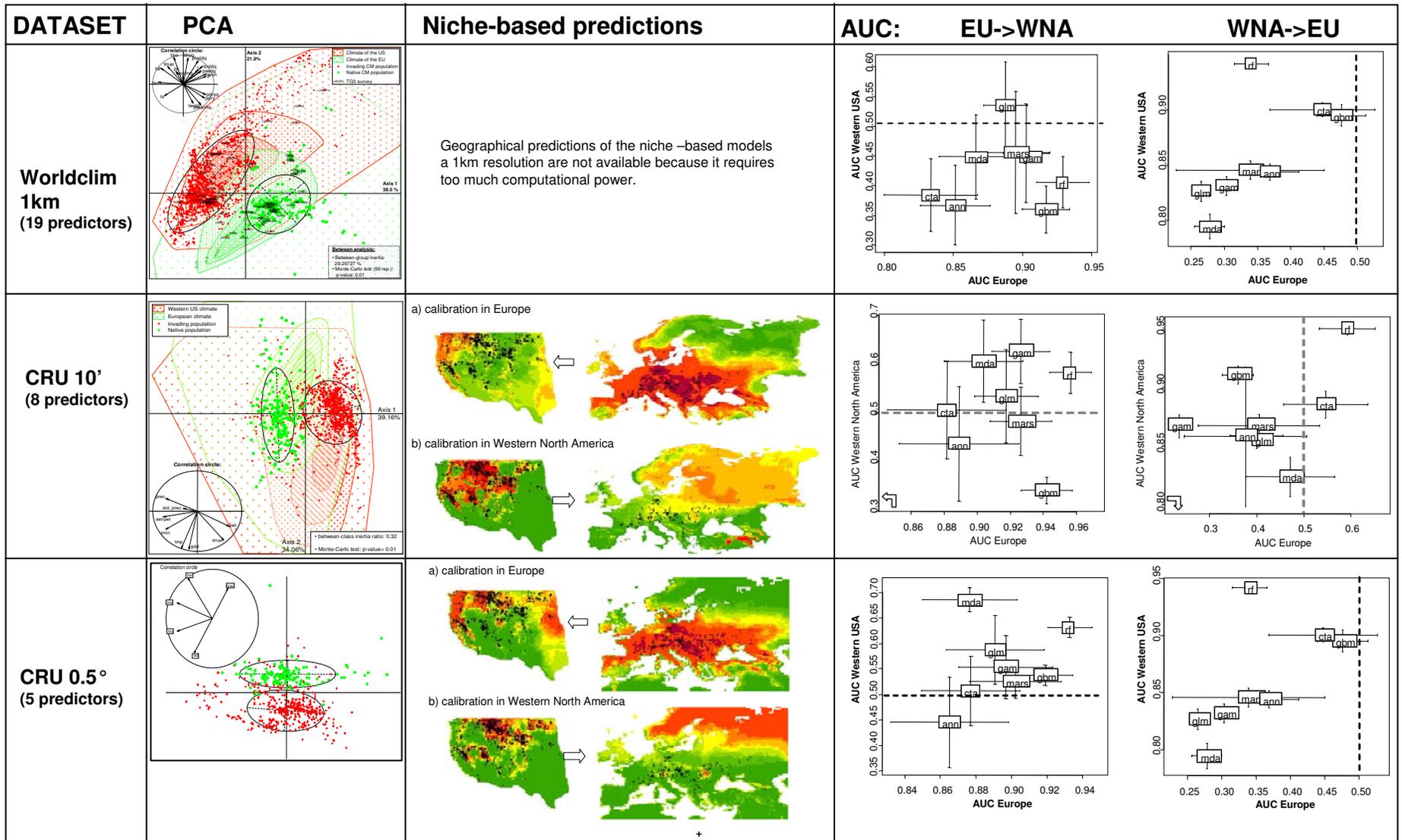
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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Figure S1 Results obtained with other climatic data sets.