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Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change

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ABSTRACT

Aim Correlative models that forecast extinction risk from climate change and invasion risks following species introductions, depend on the assumption that species' current distributions reflect their climate tolerances ('climatic equilibrium'). This assumption has rarely been tested with independent distribution data, and studies that have done so have focused on species that are widespread or weedy in their native range. We use independent data to test climatic equilibrium for a broadly representative group of species, and ask whether there are any general indicators that can be used to identify when equilibrium occurs.

Location Europe and contiguous USA.

Methods We contrasted the climate conditions occupied by 51 plant species in their native (European) and naturalized (USA) distributions by applying kernel smoothers to species' occurrence densities. We asked whether species had naturalized in climate conditions that differ from their native ranges, suggesting climatic disequilibrium in the native range, and whether characteristics of species' native distributions correspond with climatic equilibrium.

Results A large proportion of species' naturalized distributions occurred outside the climatic conditions occupied in their native ranges: for 22 species, the majority of their naturalized ranges fell outside their native climate conditions. Our analyses revealed large areas in Europe that species do not occupy, but which match climatic conditions occupied in the USA, suggesting a high degree of climatic disequilibrium in the native range. Disequilibrium was most severe for species with native ranges that are small and occupy a narrow range of climatic conditions.

Main conclusions Our results demonstrate that the direct effects of climate on species distributions have been widely overestimated, and that previous large-scale validations of the equilibrium assumption using species' native and naturalized distributions are not generally applicable. Non-climatic range limitations are likely to be the norm, rather than the exception, and pose added risks for species under climate change.

Keywords

Biotic interactions, conservation planning, ecological niche model, niche conservatism, niche shift, plant invasions, species distribution model.

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INTRODUCTION

The use of species' distributions to measure species' environmental tolerances is one of the most fundamental techniques in biogeography, and is particularly important in climate-change

ecology and invasion biology (Wiens *et al.*, 2010; Araújo *et al.*, 2011; Svenning *et al.*, 2011; Petitpierre *et al.*, 2012). This approach is based on the 'equilibrium' assumption that the locations in which species are found represent the full suite of environmental conditions in which the species can survive

indefinitely (Soberón, 2007). Although species distributions are determined by many possible biotic and abiotic factors (Soberón, 2007), the most commonly studied range limitation is climate (Araújo & Guisan, 2006; Pearson *et al.*, 2006; Araújo *et al.*, 2011; Barbet-Massin *et al.*, 2011). Research based on current native distributions has concluded that species distributions correlate with climatic conditions more strongly than with other factors, at least at coarse spatial resolutions (Thuiller *et al.*, 2004; Luoto *et al.*, 2007; Hortal *et al.*, 2010). Both conservation biology and biogeography require tools for evaluating the potential distributions of large numbers of species. Thus, models of species' climatic tolerances measured from their distributions (species distribution models, SDMs) are widely employed. SDMs are particularly used to project the locations that species will occupy following climate change (Araújo *et al.*, 2011) or following introduction outside their native range (i.e. 'biological invasions': Broennimann & Guisan, 2008; Hulme, 2012; Petitpierre *et al.*, 2012), and to understand the ecological and evolutionary forces that determine biodiversity patterns (Wiens *et al.*, 2010; Svenning *et al.*, 2011). The accuracy of this research depends on species showing niche 'conservatism' when exposed to new areas or time periods, which may not occur if the equilibrium assumption is violated.

The equilibrium assumption and niche conservatism would be violated if non-climatic factors play a strong role in limiting species' native distributions (e.g. dispersal limitations, biotic interactions and land use; Luoto *et al.*, 2007; Van der Veken *et al.*, 2007; Svenning *et al.*, 2011; Wisz *et al.*, 2013). Much of the research into the equilibrium assumption has evaluated whether climatic tolerances – measured using parts of species' current native distributions – accurately predict other parts of species' current native distributions. This approach has yielded equivocal conclusions (Leathwick, 1998; Pearson *et al.*, 2006; Randin *et al.*, 2006; Heikkinen *et al.*, 2012; Sánchez-Fernández *et al.*, 2012) and is fundamentally unsuited to assessing niche conservatism, for three principal reasons. First, even if species' current distributions correlate closely with climatic conditions, these correlations can be the outcome of non-climatic factors (e.g. biotic interactions or land use) that themselves correlate with climatic conditions (Thuiller *et al.*, 2004). Because the correspondence between climatic and non-climatic factors changes across time and space (Pearson *et al.*, 2006), even species whose distributions appear to be in equilibrium with climate might actually be able to occupy areas that appear climatically unsuitable according to the current native range. Second, because the correlations amongst climate variables will change across time and space, the tolerances measured using collinear variables in the current native range of a species cannot be extrapolated to situations with a different collinearity pattern (Dormann *et al.*, 2012). Third, evolution in environmental tolerances (sometimes called a shift in the Grinnellian or fundamental niche; Soberón, 2007) may occur when a species is exposed to a new environment (Holt *et al.*, 2005).

Recent research comparing species' native ranges with independent data obtained from naturalized or palaeo-ecological distributions supports niche conservatism for particularly wide-

spread or weedy species (Petitpierre *et al.*, 2012; Strubbe *et al.*, 2013) and highly ecologically dominant species (Pearman *et al.*, 2008). Weedy, dominant species with large range sizes are, however, more likely than other species to be at climatic equilibrium in the native range (McPherson & Jetz, 2007; Marmion *et al.*, 2009). In contrast, the species of most concern under climate change, many problematic invasives, and indeed the majority of species, are not widespread, weedy or dominant in their current native distributions (Brown *et al.*, 1996; Sax *et al.*, 2007; Araújo *et al.*, 2011). Consequently, no work has yet demonstrated whether species distributions can be used to accurately project climatic suitability for the majority of species. Furthermore, conservation efforts under climate change or biological invasions would be greatly advanced if we could provide a set of widely applicable indicators that help us to distinguish between species or circumstances in which niche conservatism should be expected.

Here, we investigate niche conservatism for species that cover the spectrums of rare to widespread, generalist to specialist (in their native range), and naturalized to invasive, by comparing the native and naturalized ranges of 51 plant species introduced from Europe to the USA. We ask whether macroecological and life-history traits, invasion histories, or the nature of the climate variables used, can inform the accuracy of distribution-based projections.

METHODS

Distribution data

In order to study a comprehensively broad range of species, we selected all species for which adequate distribution data could be obtained. We selected all European native species that are naturalized in USA states to the east of and on the western border of the Mississippi river, but studied species distributions throughout the contiguous lower 48 states of the USA ('naturalized region'). Species found in the eastern USA are well known, and are likely to be well recorded throughout the USA. From these species, we selected all species (51) whose native ranges are endemic or near-endemic to Europe (see below), and for which sufficient data were available to characterize climate niches in both the native and the naturalized region. USA distribution data were collated from multiple databases and herbaria collections (Table S1.2 in Appendix S1) and georeferenced to a 50-km UTM grid. Data on the native distribution were taken from *Atlas Flora Europaeae* (AFE; Jalas *et al.*, 1972–2010) on a 50-km UTM grid, with all grid cells in which a species was present and classed as 'native' (including archaeophytes) being included. We checked endemism to Europe using native-range data from the Germplasm Resources Information Network (USDA, 2012) and Euro+Med PlantBase (Euro+Med, 2012). The native distributions of 10 species extended into northern Africa or Turkey. For three of these species, their extra-European ranges are found only in areas for which distribution data are available in Global Biodiversity Information Facility (GBIF; available at: <http://www.gbif.org/occurrence>), which we included as part of the

native distribution. We retained the remaining ‘undersampled’ species, because they either showed no niche expansion, or have expanded into climate space that is not found in the extra-European range (assessed visually using niche-dynamic plots similar to those in Appendix S2). (See Table S1.1 in Appendix S1 for native regions and justification for inclusion.) Consequently, we are unlikely to have underestimated niche conservatism due to incomplete native distribution data. Because we excluded undersampled species that did show apparent niche shift, however, we may have overestimated niche conservatism. Consequently, we compared results for all 51 species against results for the 44 fully sampled species. The ‘native region’ refers to the European region mapped in AFE, plus the countries to which European near-endemics are also native.

In addition to the native and archaeophytic distribution, we also assessed the consequences of including additional data on European locations where the species has become naturalized within Europe but outside the historic native range [classified as ‘Introduced (established alien)’ in AFE].

Climate variables

In the absence of data on each species’ physiology and the climate variables that limit their distributions, we compared two sets of climate variables, both of which have been widely used to model plant species distributions. The first set comprises eight variables used in niche-conservatism measurements by Petitpierre *et al.* (2012): mean temperature of the coldest month (MTCM); mean temperature of the warmest month (MTWM); summed annual precipitation (SAP); ratio of actual to potential evapotranspiration (AETPET); potential evapotranspiration (PET); annual coefficient of variation in precipitation (CVPRE); mean annual temperature (MAT); and growing degree-days above 5°C (GDD5). The second set comprised three variables that represent the most basic climatic conditions that could be expected to affect species survival: MTCM, MTWM and SAP. Using many climate variables – several of which might not affect a given species’ distribution – can overfit models, underestimate climate tolerances, and underpredict potential distributions, particularly when making predictions in areas with different collinearity patterns (Araújo & Guisan, 2006; Dormann *et al.*, 2012). We compared the results obtained using three climate variables and those obtained with eight to evaluate this effect. Climate variables were averages of annual observations between 1961 and 1990 at 10-minute resolution, and were taken from New *et al.* (2002), except evapotranspiration variables, which were obtained from Ahn & Tateishi (1994). 10-minute values were averaged within each 50-km grid cell.

Calculating niche conservatism

We used two metrics of niche conservatism: (1) niche ‘expansion’, i.e. the proportion of the US distribution that falls outside the climatic conditions occupied in the native region; and (2) ‘niche shift distance’, i.e. the magnitude of the shift between the climate spaces occupied in the native and naturalized region (Fig. S1.1 in Appendix S1).

We calculated expansion following the kernel smoother (‘KS’) methodology of Petitpierre *et al.* (2012) and Broennimann *et al.* (2012). The KS approach calibrates a principal components analysis (PCA) on the entire climate space of the native region and USA simultaneously (i.e. PCA-env; Broennimann *et al.*, 2012). The first two PCA axes are used to create a gridded climate space of 100 × 100 square cells, in which each cell corresponds to a unique set of climate conditions. Species’ densities of occurrence within each climate cell were calculated using a kernel density function, which corrects for differences in the availability of climate in each region (Broennimann *et al.*, 2012). The observed expansion was the proportion of the occurrence density of the naturalized distribution that lay in grid cells outside the conditions occupied in the native distribution. We measured expansion in any part of the USA, and also only within the parts of the USA that have analogous climate space to the native region, calculated following Broennimann *et al.* (2012), using the 75% percentile of climate available in both regions. (See Fig. S1.1 in Appendix S1 for an illustration.)

Niche shift distance was measured by first defining species’ niches using the PCA described above, and then constructing a minimum convex hull polygon (‘PCA envelope’) around the native and naturalized points separately on the first two PCA axes. PCA envelopes excluded the 10% of points furthest from the centre of the species’ climate space in either distribution. After excluding the outermost 10% of points, we identified the 10% of the remaining US points that lay furthest from the native PCA envelope in climate space, and calculated the mean distance between these points and the native PCA envelope (Fig. S1.1 in Appendix S1). We calculated niche shift relative to native niche diameter in order to standardize among species. Excluding the 10% outermost points is important in order to discount the effect of rare outlying points which might reflect microclimate availability, rather than the suitability of the grid cell’s overall climate (Munguía *et al.*, 2008). In order to ensure that we had not excluded important information on species’ climatic tolerances, we compared these results with results using all species points.

Native–naturalized disequilibrium

We used KS calculations to calculate the degree to which species’ European distributions do not fill the climate space that they would be expected to, based on climate tolerances as measured in the naturalized region (‘native–naturalized disequilibrium’, NND). NND was calculated as the ratio between the occurrence density of naturalized records that occur in climate conditions that are available but not occupied within the native region (i.e. within orange pixels in PCA insets, Fig. 1) and occurrence density in the climate space occupied in the native range. (See Fig. S1.1 in Appendix S1 for further illustration.)

Indicators for niche conservatism

We investigated indicators related to two broad explanations for a lack of niche conservatism. First, the equilibrium assumption might be violated by non-climatic range limitations. Limited

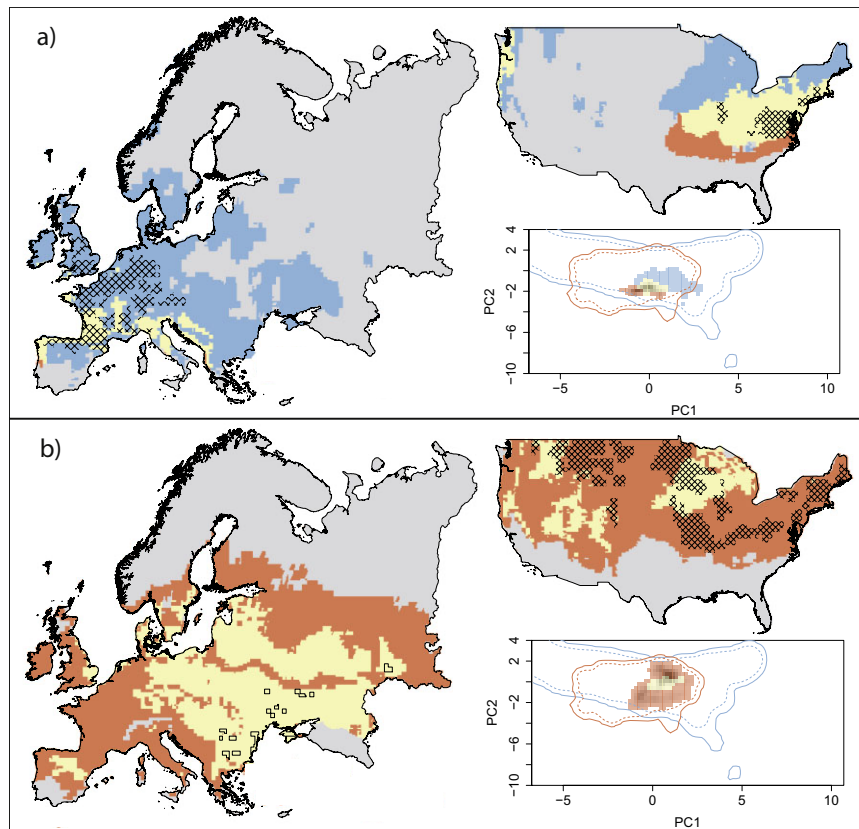


Figure 1 Illustrations of the degree of expansion in the naturalized region (USA) and native–naturalized disequilibrium (NND) in the native region (Europe) observed for two species. (a) *Helleborus viridis*, first recorded in USA in 1827, shows modest niche shift in the USA and little NND in Europe; (b) *Silene cserei*, first recorded in the USA in 1901, shows a dramatic niche shift in the USA and dramatic NND in Europe. Maps show occupied areas using hatched pixels, except Europe in panel (b) in which grid-cell outlines are used for clarity. Map colours show climatic suitability according to measurements from the native (blue), USA-naturalized (orange) and both (yellow) distributions. Inset panels show niche dynamics between native and naturalized regions for each species. Contour lines show the climate space available in each region: solid lines, all available climate space; dashed lines, 75% percentile of available climate space; blue, native region; orange, naturalized region. Grey shading areas show areas occupied in the USA, with the density of shading (from light grey to black) indicating occupancy density in the USA; yellow shading shows niche stability (i.e. climate space occupied in both the native and naturalized ranges); blue shading shows the climate space occupied in the native range that is not occupied in the naturalized range; orange shading shows expansion (climate space not occupied in the native range but which species occupy in the naturalized range). Note that to maximize clarity, the y -axis has been truncated at -10 , excluding some very small quantities of climate space only available in the native region.

dispersal ability would prevent species from occupying all climatically suitable areas (Van der Veken *et al.*, 2007; Svenning *et al.*, 2011). The effects of dispersal limitation might be distinguishable directly using metrics of dispersal ability, or indirectly using geographical range size (Van der Veken *et al.*, 2007; Baselga *et al.*, 2012). Other non-climatic range limitations include biotic interactions, land use and edaphic conditions. Current techniques and data can rarely detect these effects at coarse spatial resolutions (Wiszn *et al.*, 2013). Consequently, to investigate the severity of these effects, we used characteristics of the native range that might result from non-climatic range limitations. For instance, a large geographical range size could indicate high tolerance for non-climatic conditions and/or strong dispersal ability, which may have led to climatic equilibrium (Jetz & Rahbek, 2002; Baselga *et al.*, 2012). Occupying a narrow

range of climates, or being restricted to marginal climates (i.e. climates not commonly found throughout the native region) within Europe, could suggest strong non-climatic range limitations (Jetz & Rahbek, 2002; Baselga *et al.*, 2012), but could also be due to high specialization for those climate conditions (Franklin *et al.*, 2009; Marmion *et al.*, 2009). The second possible explanation for a lack of niche conservatism is that post-introduction evolution might alter species' environmental tolerances. Consequently, we might expect to see more niche expansion in species with short generation times that have been naturalized for long periods, owing to the greater potential for evolution after a greater number of generations. We tested these explanations using the following data.

Range size – the number of 10-minute grid cells occupied in the native range (log-transformed for analyses).

Niche breadth – niche breadth of the native range was calculated using the area of the PCA envelope surrounding the most central 90% of native distribution points in the PCA climate space of the native region.

Marginality – we used the outlying mean index (OMI), which describes the distance between the mean climatic conditions used by each species and the mean climatic conditions of the native region (ADE4; Dolédec *et al.*, 2000; Dray & Dufour, 2007). Marginality was log-transformed for analyses.

Dispersal ability – We used the classification of dispersal ability developed by Vittoz & Engler (2007) to assign the distances to which 99% of the seeds in a plant population are dispersed. Assignments are based on simple traits such as height, dispersal mode and dispersal vector.

Generation time – Species were classified as annual (including species that reproduce either annually or biennially, and species that reproduce either annually or perennially), biennial (including species that reproduce either biennially or perennially) or perennial (species that only reproduce perennially) according to the *PLANTS Database* (available at: <http://plants.usda.gov/>).

Introduction date – Differences in niche conservatism among species could be an artefact of the greater opportunity for expansion in species that have spent more time in the USA. The date of introduction or first naturalized record for each species were extracted from historical literature and accounts (i.e. floral atlases and reports from botanic gardens, societies and agricultural stations), herbarium collections and seed catalogues. Where data on introductions were not available, we used the first naturalized record, on the basis that if the species were not recorded earlier it is unlikely to have naturalized or been widely planted previously.

Analysis – We assessed the relationships between indicators and (1) niche expansion, (2) niche shift distance and (3) NND, by constructing GLMs for all potential combinations of explanatory variables. (Correlations between explanatory variables are shown in Table S3.1 in Appendix S3.) For niche expansion, we used a quasibinomial error structure with a log link function, which intrinsically accounts for sample size, i.e. USA range size. We also tested indicators and niche expansion without the effect of USA range size, but the results were not qualitatively different (Table S3.2 in Appendix S3). For the other two response variables, we used a Gaussian error structure, and weighted the regressions by USA range size. Niche shift distance was hyperbolic-sine-transformed and NND was log-transformed. In all cases, a best model subset was selected using the quasilielihood Akaike information criterion (QAIC i.e. corrected for overdispersion), and models with $\Delta\text{QAIC} < 2$ were retained.

If the likelihood for niche expansion is greater for species with narrow native ranges and niches, this could be an artefact of there being more climate space in the USA that lies outside native conditions for these species to invade, relative to species with broad native ranges and niches. We calculated each species' potential for expansion as the number of grid cells available in the gridded USA climate space that do not

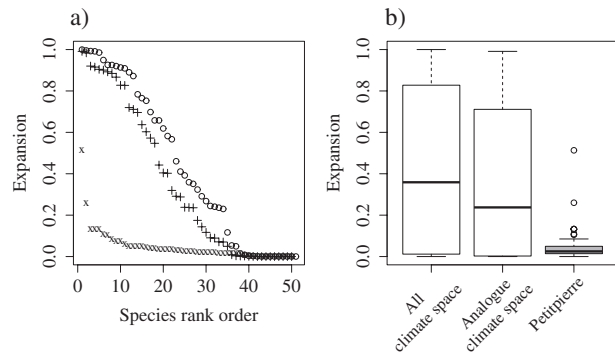


Figure 2 (a) Niche expansion (the proportion of the USA distribution that falls outside the climatic conditions occupied in the native region) is shown for each species: open circle, expansion measured in all USA climate space; +, expansion measured in analogue climate space only. For comparison, we also plot the different set of species examined by Petitpierre *et al.* (2012: Table S5), for which calculations were made in analogue climate space only, indicated by the symbol 'x'; (b) Boxplots show median, 25% and 75% percentiles, whiskers extend to $1.5 \times$ interquartile range, and points are values lying outside this range.

correspond to climatic conditions in its native range. We then measured the proportion of the potential niche expansion observed for each species (Fig. S1.1 in Appendix S1).

Chorotype – species chorotype (i.e. biogeographical affinity) can illustrate geographical barrier effects. For example, Mediterranean species could be restricted by the Mediterranean Sea and by the Alps and Pyrenees, and alpine species could be restricted by distances between mountain ranges. Continental or steppic species, on the other hand, face no obvious geographical barriers. We did not analyse the effects of chorotype, owing to sample size limitations, but used the classification to identify regions in which climatic equilibrium might be expected to be particularly low. We assigned chorotypes according to the extent of each species' distribution in each biogeographical region of the AFE region: alpine, Atlantic, boreal, continental, mediterranean, mediterranean–alpine, mediterranean–Atlantic, pluriregional (widespread or scattered across many regions) and steppic (Fig. S1.2 and Table S1.1 in Appendix S1, Roekaerts, 2002). All analyses were conducted with R 2.15.2.

RESULTS

Niche conservatism

Niche expansion beyond native climate conditions varied widely among species (Fig. 2, measured using eight variables), ranging from complete restriction of the naturalized distribution within the native climate space (expansion = 0) and complete exclusion of the naturalized distribution outside the native climate space (expansion = 1). Expansion was above 50% for 22 species, with a median of 0.36. Niche expansion within analogue climate

space was slightly less than within unrestricted climate space, but was still substantial: expansion exceeded 50% for 19 species, with a median of 0.24. (Levels of expansion for a different set of species examined by Petitpierre *et al.*, 2012, are also reproduced in Fig. 2; expansion exceeded 50% for one species, with a median of 0.03.) Including data on European grid cells where the species has naturalized within Europe but outside the historical native range did not substantially affect results, but did decrease expansion for a few species with extreme expansion values (Fig. S3.1 in Appendix S3). Expansion was reduced when measured using three rather than eight variables (Fig. S3.1 in Appendix S3; median expansion = 0.25), but was still an order of magnitude greater than that found by Petitpierre *et al.* (2012). The remainder of our results are presented with analyses using eight climate variables in order to allow comparison with other published work. When excluding the seven ‘undersampled’ species from analyses, niche expansion increased substantially (median expansion = 0.51; Fig. S3.1).

Niche shift distance also varied among species: 21 species shifted distances more than half the native niche diameter, and four shifted distances more than twice their native niche diameter (median distance = 0.4; Fig. 3b). Excluding the outermost 10% of species points in either distribution increased the niche shift distances very slightly when compared to results in which all points were included (Fig. S3.2 in Appendix S3).

Native–naturalized disequilibrium

High NND indicates that a species is absent from many areas in the native region that are climatically similar to areas occupied in the naturalized range. NND varied greatly among species: 0 for ten species, ≥ 1 for 12 species (where a value of 1 indicates that the area of NND is equal to the native range size), and with an upper limit of 7.3 (*Potentilla intermedia*). NND was positively correlated with niche expansion ($r = 0.58$, $P < 0.0001$) but not with niche shift distance, revealing that even a small niche shift can result in a large amount of NND.

Indicators of niche conservatism

The greatest niche expansion was observed for species with small range sizes, narrow niche breadths, and marginal climatic distributions in their native range (Fig. 3, Table 1). For example, *Helleborus viridis* is widespread and common in its native range, and its naturalized distribution remains almost completely within its native climate space (Fig. 1a). In contrast, *Silene cserei* is rare and fragmented in Europe, but occupies a much wider climate space in the USA. A large area in Europe appears to be climatically suitable, based on the naturalized distribution, but is not occupied (i.e. high NND, Fig. 1b). Niche shift distance and NND also correlated negatively with native range size and niche breadth, and positively with marginality (Fig. 3, Table 1). There was no clear trend in NND for species with different geographical distributions (chorotypes), but NND was noticeably high for the steppic and continental species (Fig. 3c). The time since introduction unexpectedly decreased niche expansion, niche

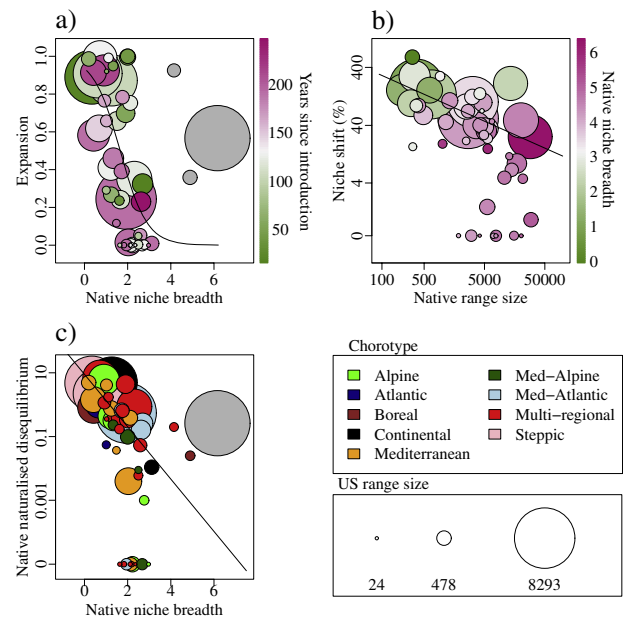


Figure 3 Examples of several indicators of niche conservatism, as assessed using different metrics of niche shift. (a) Relationship of native niche breadth with niche expansion, i.e. the proportion of the USA distribution that falls outside the climatic conditions occupied in the native region; symbol colour is scaled by number of years since introduction. (b) Relationship of native range size with niche shift distance, i.e. the magnitude of the shift between climate space occupied in the native and naturalized region, relative to the native niche diameter; symbol colour is scaled by native niche breadth (note native range size is log-transformed but x -axis labels indicate raw values). (c) Relationship of native niche breadth with native–naturalized disequilibrium; symbols are coloured according to chorotype. Grey circles in panels (a) and (c) were outliers that were not used to fit GLMs. Symbol size is scaled by the number of USA grid cells occupied. Regression lines were produced using the same methodology as for Table 1, although only the x -axis variable was examined, and are significant ($P < 0.05$).

shift distance and NND (Fig. 3, Table 1). There was no relationship between dispersal ability and either the niche conservatism metrics or NND. Generation time did not correspond to niche conservatism, even when the time since introduction was introduced as a covariate in order to look for an effect of number of generations since introduction. Indicators of niche conservatism remained similar when niche expansion in analogous climate space was considered, and when the seven ‘undersampled’ species were excluded from analyses (Tables S3.2 & S3.3 and Fig. S3.3 in Appendix S3).

There was a significant negative relationship between the proportion of potential expansion achieved and native niche breadth in all climate space ($P = 0.009$) and in analogous climate space ($P = 0.004$), and for native range size in analogous climate space ($P = 0.046$) (Fig. S3.4 in Appendix S3). The relationship was negative but (marginally) non-significant for native range size in all climate space ($P = 0.076$). These results demonstrate

Table 1 Indicators of niche conservatism. QAIC weights and parameter estimates for all explanatory variables retained in the best model subset. QAIC weights were calculated for each parameter as the sum of QAIC weights across all models in which the parameter appeared. Parameter estimates were averaged over all models in the best subset, and standard deviation is shown in parentheses. Niche conservatism metrics were calculated using eight climatic variables.

Explanatory variable	Niche expansion		Niche shift distance		Native–naturalized disequilibrium	
	QAIC weight	Model-averaged estimate	QAIC weight	Model-averaged estimate	QAIC weight	Model-averaged estimate
Log(native range size)	0.181	−0.037 (0.075)	0.434	−0.139 (0.619)	0.297	−0.188 (0.384)
Native niche breadth	1	−1.451 (0.249)	0.302	−0.137 (0.217)	0.425	−1.232 (1.172)
Log(native marginality)	0.213	0.049 (0.105)	0.223	0.024 (0.069)	0.232	0.042 (0.085)
Time since introduction	0.588	−0.004 (0.005)	0.303	−0.002 (0.003)	0.299	−0.003 (0.004)
Log(native range size) ²			0.064	−0.014 (0.042)		
(Native niche breadth) ²	0.152	−0.042 (0.084)			0.063	0.008 (0.025)
(Time since introduction) ²	0.080	0.000004 (0.0000119)				

that the relationship between niche expansion and native niche breadth (and probably native range size) is not an artefact of the greater proportional availability of climate space for the niche expansion of species with narrow native niche breadths.

DISCUSSION

The highly variable but generally low degree of niche conservatism and high degree of NND suggest that constructing SDMs with climate conditions within current native distributions will substantially underpredict the area that is climatically suitable for the majority of species following naturalization or climate change. This is particularly the case for species with small native ranges, those that occupy a narrow range of climate conditions or those that primarily occupy marginal climates in their native region. It should be noted that these trends might be influenced to some extent by phylogenetic autocorrelation, in which case taxonomic data could provide further information on the likelihood of niche conservatism. Previous analyses, using independent data for widespread or weedy species, that support the use of distribution-based projections (e.g. Pearman *et al.*, 2008; Petitpierre *et al.*, 2012) appear to have focused on the subset of species for which niche conservatism is the norm. Our findings do not necessarily contradict previous work, but suggest that such work is not applicable to the majority of species, which are not widespread or weedy in their native range. In particular, results from widespread agricultural weeds (Petitpierre *et al.*, 2012) are unlikely to be generalizable to other types of species. Agricultural weeds are likely to be at climatic equilibrium, because they have been inadvertently spread by humans within the native region and establish populations easily. This is supported by our finding that long-introduced species showed greater niche conservatism than more recent introductions (Table 1, Fig. 3). Many of the species introduced early in the colonization of the USA are agricultural weeds in Europe, accidentally introduced through seed contamination (Mack & Erneberg, 2002). These species are widely dispersed by humans in Europe, and have thus had the opportunity to fill all the

available climate space. More recently introduced plants are more likely to have been introduced deliberately (e.g. as ornamentals), and are thus less likely to have been spread widely throughout Europe.

Biogeographical studies suggest that the distributions of small-ranged species are less climatically determined than those of widespread species, but the evidence for this conclusion is generally indirect (Jetz & Rahbek, 2002; Baselga *et al.*, 2012). Conversely, when tested using current native data alone, SDMs appear to be accurate for species with small native ranges, suggesting they are climate specialists (Franklin *et al.*, 2009; Marmion *et al.*, 2009). Our results provide compelling direct evidence for the former argument: range-restricted species undergo strong non-climatic range limitations. The high accuracy of climatic SDMs for small-ranged species is thus likely to be an artefact of data limitations. Rapid post-introduction evolution is an alternative explanation, but seems unlikely to be a major factor, because none of time since introduction, generation time, or their interaction affected niche shifts (Table 1). Moreover, evolution would be expected to act similarly regardless of niche breadth. Although it is conceivable that species with narrow niche breadths could experience rapid rates of evolution in climate tolerances relative to other species (Fisher-Reid *et al.*, 2012), there is insufficient evidence to invoke this as a general mechanism. Nevertheless, we do not rule out evolution as an explanatory factor in some cases.

Although it is generally expected that non-climatic factors limit species distributions to some extent, the rationale for most climatic SDM analyses is that non-climatic effects are negligible at large scales and coarse resolutions (Thuiller *et al.*, 2004; Luoto *et al.*, 2007; Hortal *et al.*, 2010). Our results suggest that these effects are far from negligible and must be better understood. Candidate non-climatic range limitations are geographical barriers, non-climatic physical environmental features and biotic interactions (Mitchell & Power, 2003; Barbet-Massin *et al.*, 2011; Svenning *et al.*, 2011). For several of the Mediterranean species that showed high NND (Fig. 3c, Fig. S3.5 in Appendix S3), a geographical barrier effect (i.e. the Alps, Pyrenees and Mediter-

anean Sea) seems likely. For other species, such as the steppic species *Silene cserei* (Fig. 1b) and *Atriplex micrantha* and the continental species *Erucastrum gallicum* and *Spergularia echinosperma*, geographical barriers in Europe seem unlikely to be important (Fig. 3c, Fig. S3.5 in Appendix S3). Biotic limitations, which are lifted in the naturalized range ('enemy release hypothesis'), are a likely candidate for limiting these species' native distributions (Mitchell & Power, 2003; Wisz *et al.*, 2013).

There is debate over whether climatic conditions in the naturalized region that have no analogue in the native region should be included in assessments of niche conservatism (Petitpierre *et al.*, 2012; Webber *et al.*, 2012). Our opinion is that understanding the potential for species to shift into no-analogue climates is crucial for forecasts of distributions following climate change or biological invasions. Nonetheless, niche expansion within analogous climate space was almost as great as in the USA as a whole (Fig. 2), and niche expansion appears to be driven by a high degree of NND (Figs 1 & 3).

The large increase in niche expansion when using eight climate variables over using only three climate variables demonstrates the 'overfitting' caused by including climate variables that exert no real effect on the species' distribution. The magnitude of underprediction of species distributions would greatly affect management strategies for invasions or native range shifts. Selecting physiologically informed climatic variables for each species is preferable but often impossible, in which case we recommend parsimonious selection of variables.

Implications for biological invasions and for native populations under climate change

Four species in our dataset have recognized invasive impacts (according to the *Invasive Plant Atlas of the United States*; available at: <http://invasiveplantatlas.org/>): *Cerastium tomentosum*, *Coincya monensis*, *Spergula morisonii* and *Ulmus procera*. Niche expansion values for these species are 62%, 0%, 5% and 35%, respectively, underlining the difficulty of pre-introduction weed risk assessment (Hulme, 2012). In light of our results, combining both native and naturalized ranges to improve predictions of the invasive range seems sensible (Broennimann & Guisan, 2008; Gallien *et al.*, 2010). Current naturalized distributions might, however, still underestimate the climate space that could be occupied.

Our findings suggest that the direct effects of climate change on species' native distributions are likely to be less than currently predicted for some species. The species we studied have undergone niche expansion into both hotter, drier areas (suggesting that climate warming will affect their native distributions less than predicted) and cooler, wetter areas (Appendix S2). We cannot, however, quantify the frequency with which shifts into warmer or cooler conditions might generally occur, since the directions of species' naturalized niche expansions depend on the parts of the USA to which they have been introduced or been able to spread. Niche shift distance demonstrates the degree of climate change that species might be able to resist. The 12 species for which niche shift distance was equal to niche

breadth have very small native niche breadths and range sizes (Fig. 3b, Table 1). This suggests that, although erroneous predictions of local extinction under climate change might occur in parts of the native ranges of large-ranged species, a species with a small range could erroneously be predicted to go extinct throughout its entire range.

Importantly, our results do not imply that ecological concerns under climate change are unjustified. Rather, the uncertainty in future forecasts based on correlative approaches is even greater than currently anticipated. If, as our results suggest, species native distributions are substantially limited by non-climatic factors such as land use, biotic interactions and geographical barriers, these factors may restrict range shifts much more severely than is usually accounted for in forecasts. Non-climatic factors, which might themselves be influenced by changes in climate (particularly biotic interactions as communities are disturbed), will restrict range shifts or cause the extinction of current populations to a greater degree than currently anticipated.

There is considerable room for synergy in research into biological invasions and native range shifts (Sax *et al.*, 2013). First, given the likelihood that biotic interactions strongly limit species' native distributions, and the importance of enemy release in biological invasions (Mitchell & Power, 2003), it is clearly crucial to better predict both biological invasions and native range shifts. These efforts are hampered by a lack both of data and of a basis on which to predict how these factors will change across regions or time periods. Studying the range-limiting effects of biotic interactions in naturalized species would inform studies of both biological invasions and native range shifts. Second, if some of our niche-shift observations are due to rapid evolution, then management for both climate change and invasions would benefit from further investigation into the factors that promote rapid evolution during invasion. Factors that have been suggested include altered biotic interactions, habitat fragmentation/environmental heterogeneity and climatic fluctuations (Holt *et al.*, 2005). All of these are likely under global change in the native region, suggesting that evolution within native populations might mitigate the effects of climate change for a given species. However, rapid evolution of climate tolerances would have unpredictable consequences for the communities to which the species belongs (Lavergne *et al.*, 2010).

In conclusion, the possibility that species' distributions are severely out of climatic equilibrium should be suspected whenever the 'indicators' of native niche breadth or range size are small, or climatic marginality is high. Our results add to the growing body of evidence that non-climatic factors limit the distributions of many – perhaps most – species to an equal or greater degree than climate. Measuring these effects in a manner that can be repeated with relative ease for large numbers of species must become a priority.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Data sources and illustration of methods used.

Appendix S2 Illustrations of niche expansion in climate space for all study species.

Appendix S3 Supporting analyses.

BIOSKETCH

Regan Early's research addresses ecological responses to environmental change, with a dual focus on developing effective conservation strategies and on studying the principles that govern patterns of biodiversity. She is particularly interested in disentangling the effects of abiotic and biotic drivers of species distributions, how species' ecological traits determine their responses to environmental change, and in using this information to improve biodiversity models. **Dov Sax** is interested broadly in conservation biology, with a special emphasis on understanding and preventing species extinctions. Most of his work is motivated by species invasions or climate change, but he also investigates the roles of habitat loss, human exploitation and pathogens on species extinction.

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