

Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions

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ABSTRACT

Aim We explore the impact of calibrating ecological niche models (ENMs) using (1) native range (NR) data versus (2) entire range (ER) data (native and invasive) on projections of current and future distributions of three *Hieracium* species.

Location *H. aurantiacum*, *H. murorum* and *H. pilosella* are native to Europe and invasive in Australia, New Zealand and North America.

Methods Differences among the native and invasive realized climatic niches of each species were quantified. Eight ENMs in BIOMOD were calibrated with (1) NR and (2) ER data. Current European, North American and Australian distributions were projected. Future Australian distributions were modelled using four climate change scenarios for 2030.

Results The invasive climatic niche of *H. murorum* is primarily a subset of that expressed in its native range. Invasive populations of *H. aurantiacum* and *H. pilosella* occupy different climatic niches to those realized in their native ranges. Furthermore, geographically separate invasive populations of these two species have distinct climatic niches. ENMs calibrated on the realized niche of native regions projected smaller distributions than models incorporating data from species' entire ranges, and failed to correctly predict many known invasive populations. Under future climate scenarios, projected distributions decreased by similar percentages, regardless of the data used to calibrate ENMs; however, the overall sizes of projected distributions varied substantially.

Main conclusions This study provides quantitative evidence that invasive populations of *Hieracium* species can occur in areas with different climatic conditions than experienced in their native ranges. For these, and similar species, calibration of ENMs based on NR data only will misrepresent their potential invasive distribution. These errors will propagate when estimating climate change impacts. Thus, incorporating data from species' entire distributions may result in a more thorough assessment of current and future ranges, and provides a closer approximation of the elusive fundamental niche.

Keywords

Biological invasion, climate change, climatic niche, ecological niche models, *Hieracium*, invasive species.

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INTRODUCTION

Invasive species are considered one of the most serious global environmental threats (e.g. see Sala *et al.*, 2000; Thuiller *et al.*, 2007), with economic impacts reaching billions of dollars

(Sharma *et al.*, 2005). Invaders can affect ecosystem structure and function by reducing native species diversity and abundance (Wilcove *et al.*, 2000; Coutts-Smith & Downey, 2006) and modifying ecosystem processes via altered water and disturbance regimes, including fire (Mack & D'Antonio, 1998). As atmospheric

CO₂ increases and climatic zones shift, climate change has the potential to exacerbate the spread of invasive plants into previously unoccupied habitats (Dukes & Mooney, 1999; Thuiller *et al.*, 2007).

The Convention on Biological Diversity calls for preventing the introduction of invasive species (<http://www.cbd.int/convention/convention.shtml>), and this is certainly preferable and more cost effective than implementing post-establishment control and eradication procedures (Curnutt, 2000; Rejmánek & Pitcairn, 2000). One method of assessing the potential spread of non-indigenous species under current and future climates is via ecological niche models (ENMs) (Peterson *et al.*, 2003; Peterson, 2003; Rouget *et al.*, 2004; Roura-Pascual *et al.*, 2004; Thuiller *et al.*, 2005; Schussman *et al.*, 2006). These models are usually calibrated on the realized niche of species and make several assumptions including: that the best indicator of the climatic requirements of a species is its current distribution, that distributions are in equilibrium with current climate (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005), and that climate niche conservatism is maintained in both space and time (Peterson, 2003). Thus the models predict that species will only be able to establish populations in areas with similar climatic conditions as their native range. As such, it has been suggested that models based on the realized climatic niche of a species' native range may provide a useful approach to identifying its invasive potential distribution (Welk *et al.*, 2002; Peterson *et al.*, 2003; Peterson, 2003; Welk, 2004; Martinez-Meyer & Peterson, 2006; Mau-Crimmins *et al.*, 2006). Recent studies, however, have shown that invasive species do not always conserve their climatic niche, as they are able to grow and reproduce in climates other than those that they occupy in their native range (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Loo *et al.*, 2007). If the realized climatic niche is underestimated and/or differs in native versus invasive regions, then the predictive capacity of ENMs will decrease (Peterson & Holt, 2003; Welk, 2004), and models risk misrepresenting the potential for invasion (Peterson, 2005; Loo *et al.*, 2007). For example, the realized climatic niche of spotted knapweed (*Centaurea masculosa* Lam.) in its invasive North American range is different to that in its native European range, with niche differentiation occurring primarily along a water availability gradient (Broennimann *et al.*, 2007). As a result, calibration of ENMs based on native range data failed to predict the invaded distribution of this species.

There are several reasons why the realized niche of a species may not be conserved spatially or temporally. Historic and geographical constraints may prevent a species from occupying its entire fundamental niche. An example is provided by the New Zealand mudsnail, which is invasive in Australia and North America. As the mudsnail originated from a small geographical region in New Zealand, models formulated on only the data from its native range failed to adequately predict known invasions in Australia and North America, i.e. the climatic range of the snail in invaded regions was wider than in its native New Zealand (Loo *et al.*, 2007). In non-indigenous environments, release from enemies and competitors that may limit range margins in native regions may also result in a realized niche change (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007), and during the early stages of invasion a species may not be at equilibrium with its environment (Hulme, 2003; Welk, 2004). Thus, descriptions of the species–environment relationship will not be accurate because sampling across the entire gradient of environmental space in which the species could occur cannot take place (Heikkinen *et al.*, 2006). While historical and geographical constraints may influence the realized niche, evolutionary changes occurring due to genetic shift or selection operating in the introduced range may also affect the fundamental niche of species (Broennimann *et al.*, 2007; Lavergne & Molofsky, 2007). Given the potential for niche shifts, models based on data from both invaded and native ranges (i.e. closer to the species' fundamental niche) may provide a more representative range of conditions under which the species may spread (but see Welk, 2004; Mau-Crimmins *et al.*, 2006) (Fig. 1).

In this study we assessed shifts in the realized climatic niche occupied by native versus invasive populations of three species of perennial herbs in the genus *Hieracium*. We then investigated the impact of calibrating ecological niche models using data from the (1) native range (NR) only versus (2) entire range (ER) (native and invasive) on projections of current and future distributions.

METHODS

Hieracium

The genus *Hieracium* (family Asteraceae) contains over 9000 species, most of which are native to temperate and montane areas of the Northern Hemisphere. Some *Hieracium* species

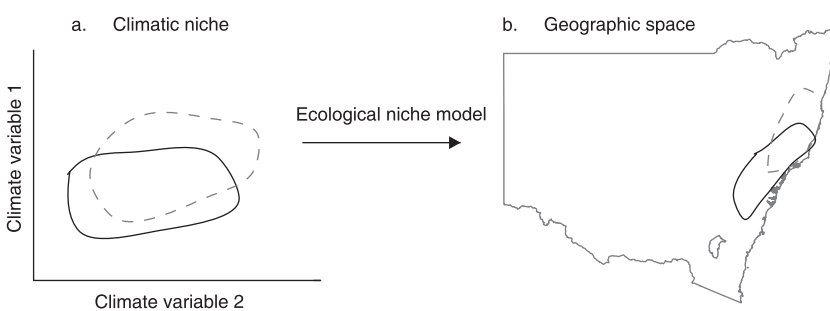


Figure 1 (a) A schematic representation of the climatic envelope of a hypothetical species in its native range (unbroken black line) and invasive range (broken grey line). Calibrating ecological niche models on data from native ranges only may misrepresent the potential geographical distribution (b).

are highly invasive, particularly in Australia, New Zealand and North America. The ability of *Hieracium* species to form dense monocultures and outcompete native species, agricultural crops and pastures in New Zealand and North America has resulted in these species being classified as emerging weeds of significance to the Australian grazing industry (Barker *et al.*, 2006). Four *Hieracium* species native to Europe have naturalized in Australia: *H. aurantiacum* L., *H. murorum* L., *H. pilosella* L. and *H. praealtum* Vill. Ex Gochnat. These species may threaten tussock grasslands and tablelands in alpine and temperate regions of eastern Australia (Barker *et al.*, 2006), and have been found in Eucalypt woodlands and alpine heathlands (Williams & Holland, 2007). Although the distributions of these four species in Australia are currently restricted, the potential threat posed by their presence has resulted in them being placed on the National Alert List of invasive species (Brinkley & Bomford, 2002).

Data sources

Current climate data were obtained from WorldClim (version 1.4) (Hijmans *et al.*, 2005) and included annual precipitation (AP), mean temperature of the coldest quarter (MTCQ), maximum temperature of the hottest month (MTHM), mean diurnal range (MDR), precipitation of the driest month (PDM) and precipitation seasonality (PS). These variables were selected as they provide an uncorrelated mix of means, extremes and seasonality. Data were downloaded at a spatial resolution of 10 min then re-projected to an equal area grid of 10 km² using a bilinear interpolation in ArcGIS (version 9.1) (ESRI, 2006). Climate scenarios for Australia were extracted from OzClim (version 2.0, <http://www.cmar.csiro.au/ozclim/index.html>) for the reference year 2030. To account for some of the uncertainty in future climates we obtained data from two climate models (CSIRO Mk2.0 and NCAR CCSM 3) as well as two emissions scenarios (A1F with high climate sensitivity and B1 with low climate sensitivity). The climate models were selected because (1) objective analyses of CSIRO MK2.0 suggested that it provides good simulations of current climate across Australia (A. Pitman, personal communication.) and (2) simulations from NCAR are commonly used in impacts assessments and provide an independent source of data to CSIRO MK2.0. The B1 storyline describes a convergent world with a global population that peaks in mid-century and declines thereafter but with rapid changes in economic structures toward a service and information economy and the introduction of clean and resource-efficient technologies. Cumulative CO₂ emissions from 1990 to 2030 total 369.9 GtC, and human population is set at 8.196 billion. The A1 storyline describes a future world of very rapid economic growth, global population structure the same as the B1 storyline and the rapid introduction of new and more efficient technologies. The A1F scenario focuses on maximum fossil fuel use. By 2030 human population is estimated to be 8.122 billion with cumulative CO₂ emissions from 1990 totalling 420.9 GtC (Nakicenovic *et al.*, 2000). CSIRO Mk2 and NCAR estimate an increase in Australia's annual mean temperature of 0.48 and 0.47 °C, respectively, under the B1 low climate sensitivity scenario by 2030, and 1.00 and 0.97 °C under the A1F high climate sensitivity scenario.

Distribution records of the native and invasive ranges of *H. aurantiacum*, *H. murorum* and *H. pilosella* were downloaded from a variety of online databases, including the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>), Australia's Virtual Herbarium (AVH, <http://www.flora.sa.gov.au/avh/>), Arctos (<http://arctos.database.museum/home.cfm>), Eunis (<http://eunis.eea.europa.eu/>) and E-Flora BC (<http://www.eflora.bc.ca/>). Insufficient distribution records were available to model *H. praealtum*. The Alexandria Digital Library (<http://www.alexandria.ucsb.edu/>) was used to determine, where possible, the latitude and longitude of records that were missing coordinate data. Records from several countries known to contain the three *Hieracium* species were excluded as coordinates could not be determined (*H. aurantiacum*: Romania; *H. murorum*: Slovenia, Romania, Portugal; *H. pilosella*: Croatia). In total, the data bases yielded 2684, 11237 and 29404 records with coordinate data for *H. aurantiacum*, *H. murorum* and *H. pilosella*, respectively. To reduce the impact of spatial autocorrelation we re-projected location records to a resolution of 10 km² and removed duplicate records. Similarly, as the majority of records came from Austria, France and Germany, we randomly reduced these by 50%, thereby decreasing the potential bias that may occur as a result of these areas being over-represented in the model calibration. A total of 1088, 1281 and 2721 records for *H. aurantiacum*, *H. murorum* and *H. pilosella* remained, representing the entire range (ER) of each species. Of these, 505, 33 and 285, respectively, represented invasive populations.

Locations where species are known *not* to occur are not included in the data bases examined. As absence data were required for the ecological niche models, pseudoabsences were generated. To avoid the selection of false absences (i.e. locations that lie within the climatic tolerance of the species but where the species has not been recorded because of insufficient surveying, dispersal limitations or biotic constraints) we selected pseudoabsences from sites that lay outside the species' known climatic envelope (Austin & Meyers, 1996; LeMaitre *et al.*, 2008), as defined by the six climate variables; AP, MTCQ, MTH, MDR, PDM and PS. The geographical distribution of each species' climatic envelope was mapped in ArcGIS, and locations outside of this region were randomly selected as pseudoabsences. The number of pseudoabsences selected equalled the number of presence records for each species multiplied by 10. Two sets of pseudoabsences were created for each species based on location data from the (1) native ranges only and (2) species' entire ranges. To ensure that results were not dependent on a single selection of pseudoabsences, we assessed the accuracy of the SDMs against 10 alternative sets of pseudoabsences.

Climatic niches of native and invasive ranges

Following Broennimann *et al.* (2007), we used principal component analysis (PCA) in the R CRAN library 'ade4' to quantify the positions of native and invasive climate niches. The magnitude and statistical significance of differences between the native and invasive occurrence clouds on the PCA graph were assessed using a between class analysis, which yielded a between class inertia ratio.

The significance of this ratio was further tested by conducting 99 Monte Carlo randomizations.

Ecological niche models

Alternative ecological niche models have different levels of accuracy under different circumstances (Elith *et al.*, 2006) and there is no single 'best' method. Using a single modelling technique does not provide any information as to whether that method gives the best predictive accuracy for the data set used (Araújo & New, 2007). Thus, multiple ENMs can be used to create an ensemble of simulations enabling a range of projections to be explored (Thuiller, 2004; Araújo & New, 2007). To model species' distributions, we used eight statistical techniques available in the BIOMOD package (version 2006.01.26) developed by one of the authors (Thuiller, 2003; Thuiller, 2004; Araújo & New, 2007). These consisted of two regression methods (GAM: generalized additive model, GLM: generalized linear model), three machine learning methods (ANN: artificial neural networks, GBM: generalized boosted model, RF: random forests), two classification methods (CTA: classification tree analysis, MDA: mixture discriminant analysis) and a surface range envelope (SRE). Models were calibrated with data from (1) the realized niche of each species' entire range (i.e. native and invaded – ER) and (2) the realized niche of native ranges only (NR), as defined by the six climatic variables. Presence/pseudoabsence data were randomly divided into two subsets with 70% of records used to calibrate the models and the remaining 30% of records used to evaluate the predictive power of each model using the area under the receiver-operating characteristic (ROC) curve and Cohen's kappa statistic. Probabilities of occurrence derived from all models (except SRE) were transformed into presence/absence data using the area under the ROC curve (AUC). The calculation of ROC curves traditionally requires both presence and absence data. If true absence data are unavailable and pseudoabsence or background points are used in their place, then the maximum achievable AUC is less than 1 (Wiley *et al.*, 2003; Phillips *et al.*, 2006). We applied a conservative classification where $AUC < 0.8$ is a poor or null model; $0.8 < AUC < 0.9$ is fair; $0.9 < AUC < 0.95$ is good and $0.95 < AUC < 1.0$ is very good (Thuiller *et al.*, 2006). Models with a kappa < 0.6 were classified as poor or null; $0.6 < \text{kappa} < 0.8$ as fair; $0.8 < \text{kappa} < 0.9$ as good and > 0.9 as very good.

Models calibrated with (1) NR data and (2) ER data were projected onto current European, North American and Australian climate surfaces, as well as future Australian climate surfaces.

A 'frequency histogram' approach, with models being given equal weights, was used to create ensembles of model projections (see Marmion *et al.*, 2009) using ArcGIS. Thus, areas classified as suitable by the majority of the models can be identified.

RESULTS

Climatic niche shifts across native and invasive ranges

A principal components analysis was conducted to reduce the dimensionality of each species' realized climatic niche. The first

two axes of the PCA were primarily associated with temperature and moisture availability, respectively. Together these axes explained 65–69% of variation in the climatic niches. The PCA graphs for each species show that the niche centroids of native and invasive populations differ strongly (between class inertia ratio of 36%, $P < 0.01$, for *H. aurantiacum*; 5%, $P < 0.01$ for *H. murorum*; 19%, $P < 0.01$ for *H. pilosella*) (Fig. 2). For *H. murorum*, the climatic niche of invasive populations is primarily a subset of that of its native range. In contrast, the climatic niches of invasive populations of *H. aurantiacum* and *H. pilosella* differed substantially from their native populations. For each species, a number of invasive populations occurred in conditions for which there is no current climate analogue in Europe.

Sufficient location data were available to compare invasive populations of *H. aurantiacum* and *H. pilosella* located in western North America, eastern North America, and Australia and New Zealand. As shown in Fig. 2, the climatic space occupied by the two species across these invasive regions differs: populations in eastern North America realize a climatic niche that is mostly outside that of native populations. For *H. pilosella*, this represents a shift to wetter conditions while for *H. aurantiacum*, the shift is to warmer, wetter conditions. Populations of *H. aurantiacum* in western North America have the broadest climatic niche, and generally occur in warmer conditions than native populations. In contrast, western North America populations of *H. pilosella* occupy a subset of the native range climatic niche. Populations in Australia and New Zealand occupy a climatic niche more similar to their native ranges than to those of North American populations.

Current range projections

The accuracy of the eight ENMs was assessed using both threshold-dependent (kappa) and threshold-independent methods (AUC). Model accuracy was consistently high, with most AUC and kappa scores exceeding 0.95 and 0.9, respectively (exceptions were ANN and MDA which scored 'good' in several runs). These results were irrespective of the selection of pseudoabsence points. Across 10 alternative selections of pseudoabsence points, the standard deviation of the AUC scores was typically less than 0.01 (exceptions were ANN and RF where the standard deviation was < 0.03). More variation occurred across the kappa scores with standard deviations typically less than 0.05, although this increased up to 0.09 for ANN.

The inclusion of invasive range data had little impact on the overall size of the projected European distributions for the three *Hieracium* species: differences primarily lay in greater consensus achieved by the eight ER models (Fig. 3). This was particularly so for *H. aurantiacum* with few NR models predicting areas around Romania as suitable. Projected distributions for all three species included large regions of eastern Europe for which few records exist.

In contrast to native ranges, projected North American and Australian distributions for the three species varied substantially. NR models projected substantially narrower ranges that, for the most part, failed to capture the known distributions of these species (Fig. 3). Invasive populations were correctly predicted by a minimum of two ENMs calibrated with ER data, with 78%

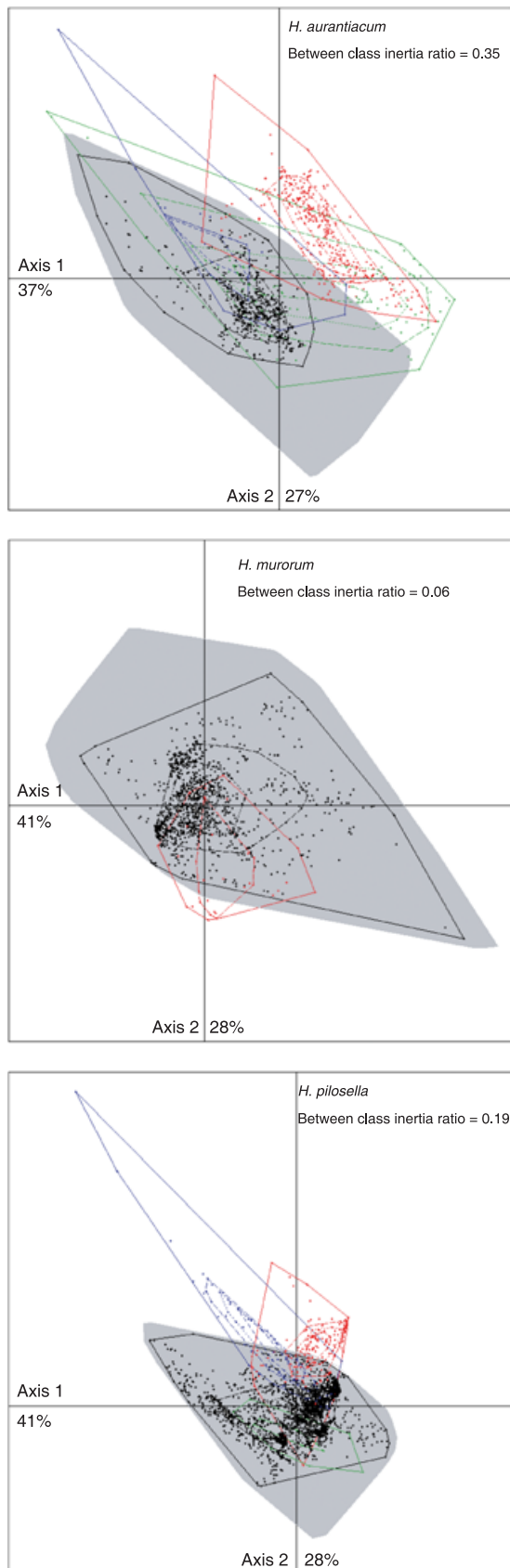


Figure 2 Comparison of the native (1 = black) and invasive (2–4 = coloured) climatic niches of three *Hieracium* species. A PCA was conducted on six climatic variables. A between class analysis

(*H. aurantiacum*), 16% (*H. murorum*) and 79% (*H. pilosella*) of these populations predicted by all eight ENMs (Fig. 4). Conversely, 64% and 23% of invasive populations of *H. aurantiacum* and *H. pilosella* failed to be correctly predicted by any of the NR models.

Projections of Australian ranges under future climates

The consensus across ENMs was for a decrease in the Australian distributions of the three *Hieracium* species in response to climate change. For ER models, averaged across the four climate scenarios and the eight ENMs, distributions for *H. aurantiacum*, *H. murorum* and *H. pilosella* were projected to decrease 15%, 9% and 9%, respectively. For NR models they decreased by 11%, 10% and 10% (Fig. 5). Thus, the use of NR or ER data to calibrate models had little impact on the *proportion* by which ranges were projected to decrease. As with current distributions, however, substantial differences occurred in the overall size of projected distributions, with NR models predicting very limited ranges (Fig. 6). For example, areas identified as suitable by at least five of the eight NR models were 93%, 50% and 47% smaller than when ER models were used, for *H. aurantiacum*, *H. pilosella* and *H. murorum*.

DISCUSSION

Niche change across native and invasive ranges

Three species of *Hieracium*, native to Europe and invasive in Australia, New Zealand and North America, occupy different climatic niches in their invasive versus native ranges. Climatic niches of invasive populations also vary across broad geographical regions. Furthermore, numerous invasive populations occur in areas for which there is no climate analogue in Europe (Fig. 2). Two general hypotheses can be put forward to explain these results: barriers to the native range may not be present in the invaded range, and/or the climatic tolerances of invasive populations may have changed as a result of local adaptation, genetic drift or phenotypic plasticity.

In their native range, biotic constraints (such as competitors, herbivores, parasites and pathogens), historical and land use legacies, dispersal limitations and geographical barriers may prevent species from occupying larger climatic ranges. The release that occurs due to the absence of these constraints in novel regions may enable species to occupy environments different to their native ranges. Release from enemies and disease are two of several reasons suggested for the differences in the climatic niche

tested the magnitude and significance of the occurrence clouds, yielding a between class inertia ratio which was further tested using 99 Monte Carlo randomizations. For *H. aurantiacum* and *H. pilosella* sufficient occurrence data were available to test for differences across the occurrence clouds of invasive populations in eastern North America (2, red), western North America (3, green) and Australia/New Zealand (4, blue). Graded lines represent convex hulls enclosing 75% and 100% of occurrence records. European climate space is shown in grey.

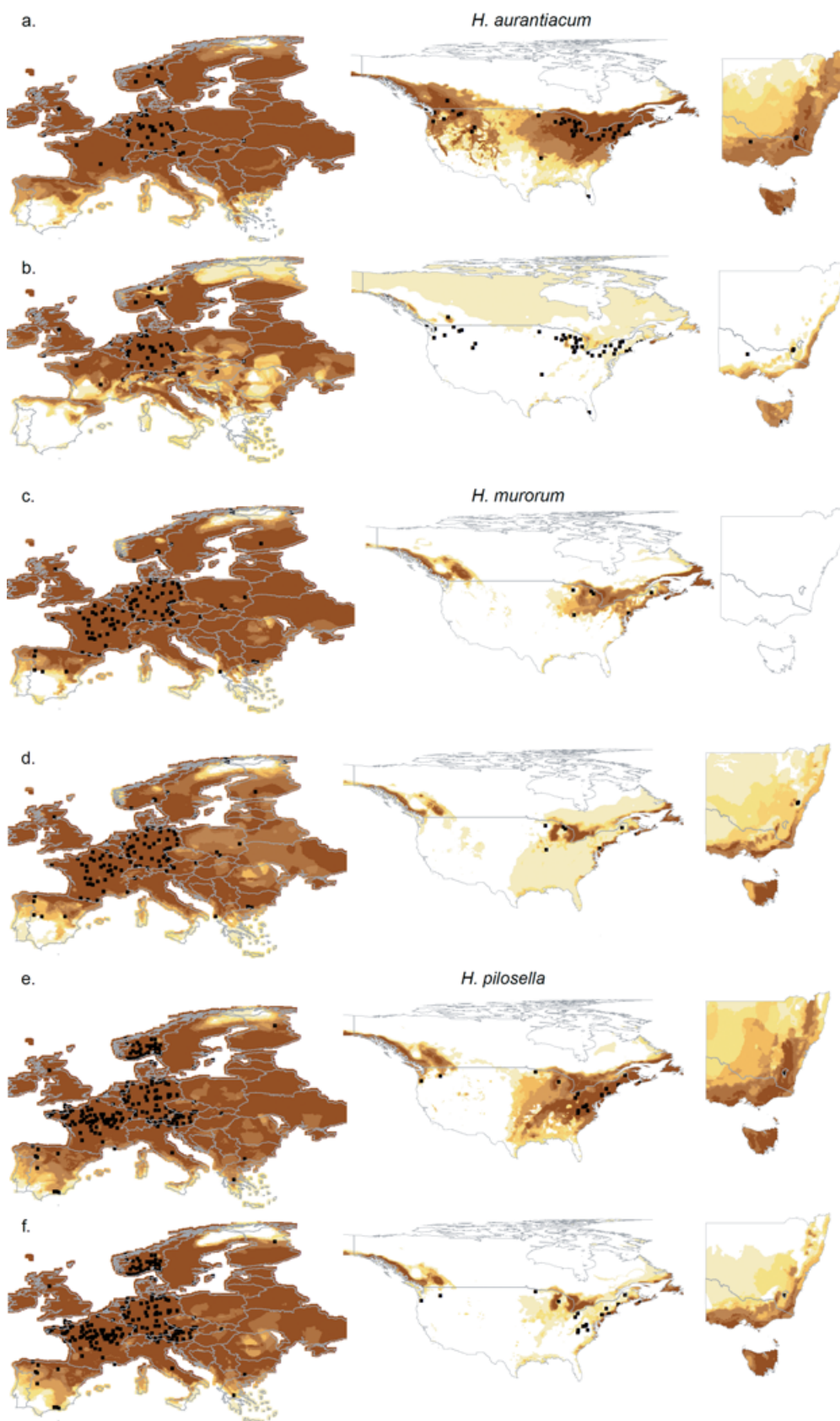


Figure 3 Current European, North American and Australian (New South Wales) distributions for three *Hieracium* species, projected by eight ecological niche models calibrated with entire range (ER) data (a, c, e) and native range (NR) data (b, d, f). Darker colours indicate greater agreement among ecological niche model (ENMs). Black circles represent the known locations of each species (for ease of reading, a random sample of 10% is shown).

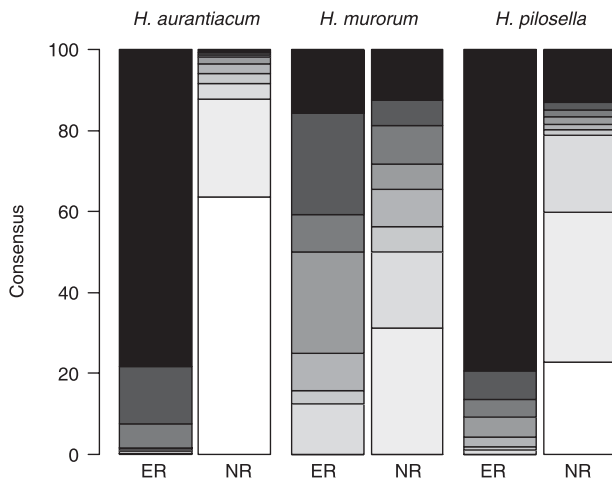


Figure 4 The proportion of known invasive populations of three *Hieracium* species correctly predicted by eight ecological niche models calibrated with data from species' entire ranges (ER) or native ranges (NR). The grey scale indicates consensus among models where white identifies populations that none of the models predicted as present while dark grey represents populations correctly predicted by all models.

occupied by fire ants in North America compared to their native range in South America (Fitzpatrick *et al.*, 2007). Several specialist insect taxa have been recorded on some Hawkweed species in Europe and may cause significant damage (Sároszpataki, 1999). However, few specialists appear to feed on *H. pilosella* in its native range (Sároszpataki, 1999). Similarly, although a variety of generalist herbivores are found on Hawkweeds in New Zealand, none of these cause serious damage, and specialist taxa do not occur on these plants (Syrett & Smith, 1998). In the Nordic countries, geographical barriers to the migration of numerous *Hieracium* have been identified (Tyler, 2000); however, there is generally little known about the factors limiting range margins of *Hieracium* in other regions.

Successful invaders may expand their range into varying habitats by undergoing local adaptations or as a result of genetic drift (Callaway & Ridenour, 2004; Lavergne & Molofsky, 2007). The genus *Hieracium* is extremely complex, resulting from recent speciation, hybridization, polyploidy and diverse reproductive strategies (Trewick *et al.*, 2004). Populations of *H. pilosella* in New Zealand have a high degree of genetic and genome size variation as a result of interspecific hybridization. The polymorphic nature of this species has resulted in a wide range of morphotypes and its invasive success in New Zealand has been attributed to its genetic variability (Morgan-Richards *et al.*, 2004). In contrast to *H. pilosella*, the genetic diversity of *H. aurantiacum* throughout its invasive range in North America and its native range is very small; this species has an unusually high proportion of asexual offspring and Loomis (2007) asserted that global populations of *H. aurantiacum* may be clones. The ability of this species to maintain populations under various conditions may be the result of phenotypic plasticity (Loomis, 2007) rather than from rapid adaptation. Low levels of genetic variability also limit local

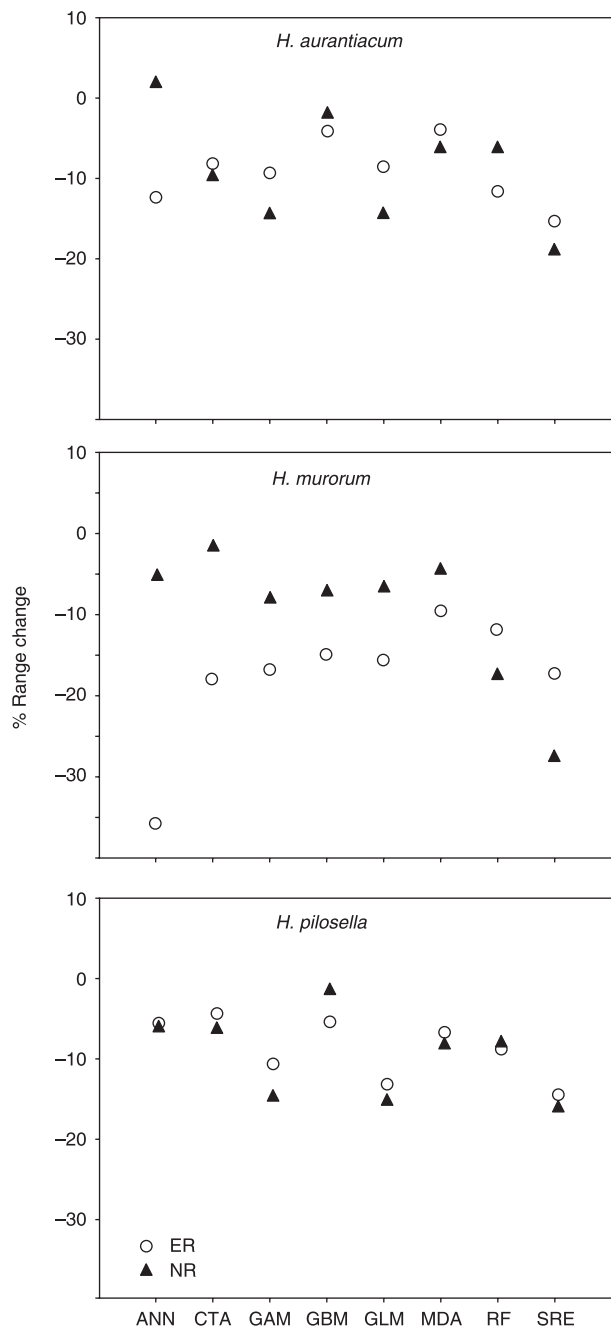


Figure 5 Percentage change in the size of the projected Australian distribution of three *Hieracium* species for 2030 (averaged across four climate scenarios, i.e. two climate models \times two emission scenarios). Eight models were used to project distributions using either data from each species' entire range (ER = circles) or native range only (NR = triangles).

adaptation within populations of *Verbascum thapsus*, an invasive perennial of North America. The success of this species across a wide environmental gradient (from mediterranean to alpine climates) is attributed to phenotypic plasticity (Parker *et al.*, 2003).

While various hypotheses can be invoked to explain niche change among the three *Hieracium* species, an alternative

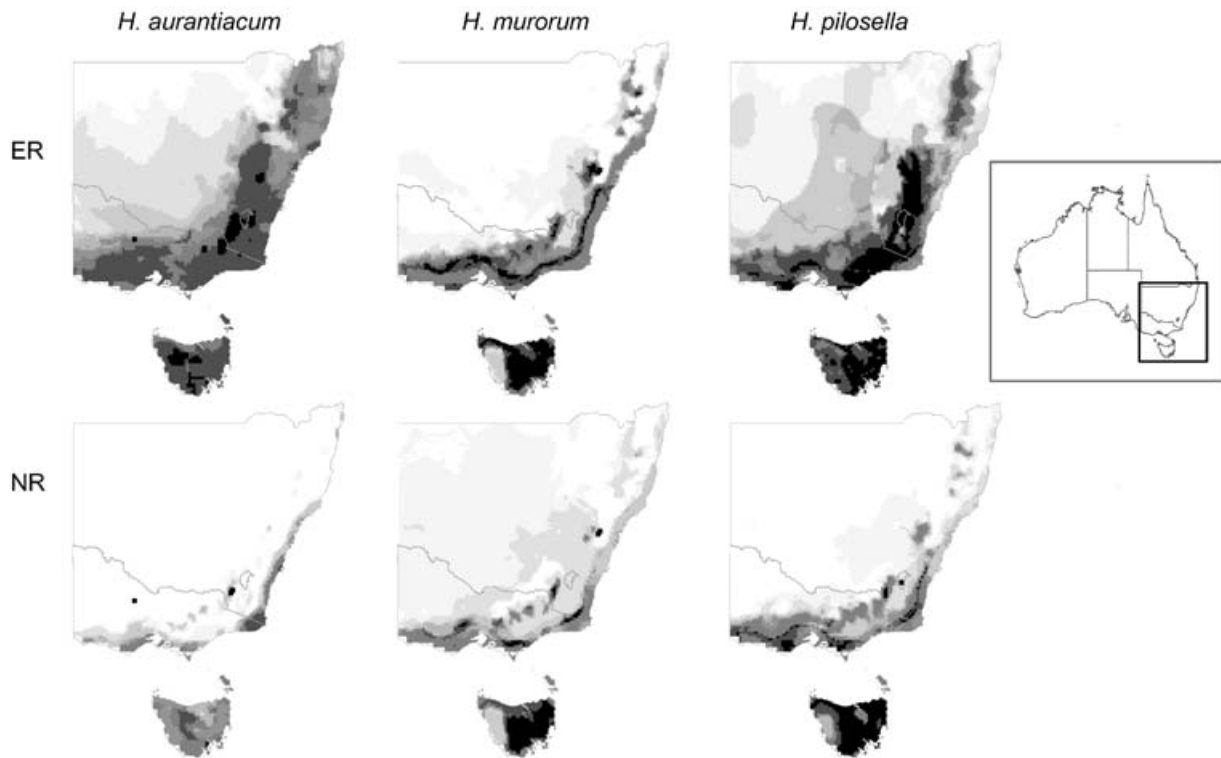


Figure 6 Future (2030) Australian (New South Wales) distributions of three *Hieracium* species derived from eight ecological niche models. The grey scale indicates model agreement of habitat suitability, where darker colours represent more models projecting that area as suitable. Models were calibrated using data from species native regions only (NR) and data from species entire ranges (ER).

explanation is that these shifts are simply an artefact of the accuracy and availability of species location data, and the scale of our study. Our study assumed that the location data used are representative of the actual distribution of each species. Similarly, we assumed that all invasive populations have been recorded. Violation of either of these assumptions will clearly influence our results. Apparent niche shifts may also be scale dependent, and it is unknown to what extent the microclimate of invasive populations differs from that of the coarse (10 min) scale used in this study. However, we believe that a change in the realized niche is the most likely explanation, as there are several examples of invasive species confined to certain habitats due to land use or competitors in their native range (i.e. fire ants (Fitzpatrick *et al.*, 2007), ice fig, *W. Thuiller*, personal observation). These species thus occupy a relatively small amount of their physiological fundamental niche, and have become highly aggressive invaders when introduced to new habitat types, released from native range pathogens or competitors, and/or further distributed by humans. The ice fig (*Carpobrotus edulis*) is, for instance, confined to natural areas in the Cape Floristic Region in South Africa but has spread dramatically around the globe principally due to its use by humans for horticulture.

In a more pragmatic sense, such realized niche change offers promising avenues to investigate the true potential ecological limits of species without resorting to transplant experiments or experimental manipulations. In theory, the sum

of all these expressed realized niches should provide the closest possible determination of the fundamental niche of the species.

Change in realized niche and ecological niche modelling

Ecological niche models calibrated on the realized climatic niche of native ranges have been used to predict species distributions in invasive regions (Peterson *et al.*, 2003; Peterson, 2003; Martinez-Meyer & Peterson, 2006; Ficetola *et al.*, 2007). The efficacy of this approach will depend on whether the expressed realized climatic niche in the invasive range is the same as that in the native range. Should the native range occupy only a subset of the entire climatic space realized by an invasive species, this approach will not capture the full invasive potential of these species (Broennimann *et al.*, 2007; Estrada-Peña *et al.*, 2007).

The impact of using a subset of the realized niche to model species distributions is demonstrated clearly by projections derived from Species Range Envelope (SRE) model. This method, commonly known as BIOCLIM, interpolates a species' bioclimatic envelope, which is a summary of the climate at locations from where the species has been recorded. The SRE model describes the climatic envelope of a species as a rectilinear volume, that is, it suggests that a species can tolerate locations where values of all climatic parameters fit within the extreme values of its climate envelope. Thus, if the entire climatic envelope is not captured

(e.g. if NR data only are used in model building rather than ER data), then the predicted distribution will not cover all locations that are climatically suitable for the species (Fig. 1): distributions for the three *Hieracium* species predicted by SRE models were substantially smaller when NR data only were used to calibrate models.

While we have advocated using ER data to model the global and Australian distributions of these species, *H. pilosella* provides an interesting example where the climatic niches of invasive populations in western and eastern North America do not overlap (Fig. 2). What data should be used to project invasive distributions in these two regions? Without experimentation or reciprocal transplants to determine fitness of individuals from the eastern populations grown under conditions analogous to western North America, or vice versa, it is unclear whether ER data or a subset of this would produce the most reasonable distribution models. However, given the genetic variability of this species in New Zealand, the use of ER data would provide a 'worst case' scenario.

By 2030, climatically suitable habitat for three species of *Hieracium* in Australia is estimated to decrease. Although similar decreases in the ranges of the *Hieracium* species were predicted regardless of the location data used, distributions obtained from NR models were 47–93% smaller than those from ER models: NR models suggest that climatically suitable habitat for *H. aurantiacum* on the Australian mainland will almost completely disappear within the next few decades. Thus, consistent with Broennimann & Guisan (2008), we found that underestimations or misrepresentations of species' current ranges due to different expressions of realized niches will have cascading impacts on projections of future distributions.

For all three *Hieracium* species, range decreases resulted from a contraction of range margins to higher elevations or latitudes. Current potential distributions of these species already incorporates the highest elevation areas in Australia, and future increases in temperature and decreases in precipitation in the south-east would be expected to result in further contractions. However, these species are yet to realize their full geographical range in Australia and substantial climatically suitable habitat remains currently available.

Intermodel comparisons and ensembles of model projections

Modelling species distributions requires the selection of a technique(s) from an increasing number of alternatives (Elith *et al.*, 2006). Although it is generally accepted that presence/absence models result in more accurate projections compared to presence-only models (Brotons *et al.*, 2004), there is no single technique that is consistently superior to others (Elith *et al.*, 2006; Heikkinen *et al.*, 2006; Pearce & Boyce, 2006). To an extent, the accuracy of different models may vary with the characteristics of individual species (Thuiller, 2003; Segurado & Araújo, 2004; Luoto *et al.*, 2005), and small differences between current distributions derived from alternative models can be magnified when projecting ranges under future climates (Thuiller, 2003). Several

authors have suggested projecting species distributions using more than one ENM, allowing uncertainty among models to be addressed (Araújo *et al.*, 2005; Thuiller *et al.*, 2005; Lawler *et al.*, 2006; Araújo & New, 2007). This is analogous to using multiple climate change scenarios to explore the uncertainty in future climates. In this study, although there was a general agreement in the projections derived from CTA, GAM and GLM, projections of other models diverged from each other, and the ability of models to extrapolate was also species-specific. Furthermore, there was a tendency for some models to predict larger distributions than others (e.g. ANN and RF). Thus, consistent with previous studies (Thuiller, 2004; Lawler *et al.*, 2006), we found substantial differences among projections of current and future distributions made by the various ENMs we used, highlighting the importance of using more than one technique to model species' distributions.

While the AUC and kappa values of the eight SDMs ranged from 'good' to 'excellent', this may be an artefact of our method of generating pseudoabsences where we deliberately included areas that were climatically distant from the presence locations. This approach would increase the rate of well-predicted absences and result in higher AUC scores: the more climatically distant the absences, the better they will be predicted with a bad model (Lobo *et al.*, 2007). The appropriateness of using AUC scores to assess the accuracy of species distribution models has recently been questioned (Lobo *et al.*, 2007) and improved methods of model evaluation have been called for (Araújo & Guisan, 2006). However, to the best of our knowledge, no alternative measures are available and a plethora of papers have conversely championed these accuracy measures (e.g. Fielding & Bell, 1997; Pearce & Ferrier, 2000).

CONCLUSIONS

There is a growing body of literature demonstrating that some species occupy different climatic niches when they move into novel regions. Failure to take this into account when projecting distributions can result in underestimation of potential invasive ranges. This in turn can affect forecasts of future range changes and has clear implications for invasive species management. We suggest that the realized climatic niche of both native and invasive ranges should be explored before modelling. Furthermore, care must be taken when exploring the potential for the spread of species in invasive regions, as these species may not be at equilibrium with climate and niches may continue to expand. If additional areas are invaded, ENMs should be refined to include this new information. Our results also suggest that modelling non-invasive species' distributions based on a subset of location records may result in similar under-representations of current and future distributions.

Finally, we suggest that further investigations be conducted to measure and sum the expressed realized climatic niche of notorious invasive species, thus identifying, as closely as possible, their fundamental niche. We may discover that the invading capacity of species is simply a reflection of the width of their fundamental niche. This could help to explain the failure of traditional comparative analyses to give a functional prototype of the perfect invader.

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