

Contrasting spatio-temporal climatic niche dynamics during the eastern and western invasions of spotted knapweed in North America

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ABSTRACT

Aim The spotted knapweed (*Centaurea stoebe*), a plant native to south-east and central Europe, is highly invasive in North America. We investigated the spatio-temporal climatic niche dynamics of the spotted knapweed in North America along two putative eastern and western invasion routes. We then considered the patterns observed in the light of historical, ecological and evolutionary factors.

Location Europe and North America.

Methods The niche characteristics of the east and west invasive populations of spotted knapweed in North America were determined from documented occurrences over 120 consecutive years (1890–2010). For this investigation, the 2.5 and 97.5 percentiles of values along temperature and precipitation gradients, as given by the two first axes of a principal components analysis (PCA), were calculated. We additionally measured the climatic dissimilarity between invaded sites and the native niche using a multivariate environmental similarity surface (MESS) analysis.

Results Along both invasion routes, the species established in regions with climatic conditions that were similar to those in the native niche. An initial spread in ruderal habitats always preceded spread in (semi-)natural habitats. In the east, the niche gradually increased over time until it reached limits similar to the native niche. Conversely, in the west the niche abruptly expanded after an extended time lag into climates not occupied in the native range; only the native cold niche limit was conserved.

Main conclusions Our study reveals that different niche dynamics have taken place during the eastern and western invasions. This pattern indicates different combinations of historical, ecological and evolutionary factors in the two ranges. We hypothesize that the lack of a well-developed transportation network in the west at the time of the introduction of spotted knapweed confined the species to a geographically and climatically isolated region. The invasion of dry rangelands may have been favoured during the agricultural transition in the 1930s by release from natural enemies, local adaptation and less competitive vegetation, but further experimental and molecular studies are needed to explain these contrasting niche patterns fully. Our study illustrates the need and benefit of applying large-scale, temporally explicit approaches to understanding biological invasions.

Keywords

Centaurea stoebe, herbarium records, human disturbances, invasion routes, niche conservatism, niche limits, North America, plant invasions, spotted knapweed, temporal data.

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INTRODUCTION

Despite the rapidly accumulating literature on biological invasions, including ever-emerging new hypotheses and meta-analyses, ecologists still lack a detailed understanding of why specific plant invasions occur, making it difficult to predict which species may become invasive and where (Dietz & Edwards, 2006; Gurevitch *et al.*, 2011). Many different mechanisms promoting invasion have been proposed and tested (Dietz & Edwards, 2006), with contradictory findings. Inconsistencies in these findings may be because investigations of mechanisms promoting invasions have been performed indiscriminately at various invasion phases (e.g. lag phase, primary invasion and secondary invasion), locations (e.g. core area of the native range, introduction area and invasion front), habitat types and environmental conditions, each of which is likely to show different invasion dynamics. Accounting for these changes over time holds the promise of a better spatial and temporal understanding of invasions (Dietz & Edwards, 2006), but to our knowledge has not been tried so far. For this to be accomplished, integrative studies are needed that assess key ecological factors throughout the course of invasions.

One key determinant of invasions is the pre-adaptation of species to the environment in the new range, as determined by their climatic niche (Maron *et al.*, 2004; Treier *et al.*, 2009; Di Febbraro *et al.*, 2013). Since the development of niche-based species distribution modelling (SDM; Guisan & Thuiller, 2005; also called ecological niche models, ENM; Peterson *et al.*, 2011), our understanding of abiotic components driving invasions through space has improved considerably (e.g. Gallien *et al.*, 2010). An increasing number of studies have used SDMs (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Rödder *et al.*, 2009; Medley, 2010; Petitpierre *et al.*, 2012) or related tools (e.g. Broennimann *et al.*, 2012) to investigate the niche of invader species and assess whether it is conserved between ranges. However, no investigation has been performed on the mode and tempo of niche changes along invasion routes.

A good model system for this investigation is spotted knapweed (*Centaurea stoebe* L.), a plant native to south-east and central Europe and highly invasive in North America (Sheley *et al.*, 1998). The first records of the species in North America indicate that the species was introduced in the USA near Westford, Massachusetts, in 1884 (Invasive Plant Atlas of New England; <http://www.eddmaps.org/ipane>; accessed on 13 December 2010) and at the border of the USA and Canada in Victoria, British Columbia, in 1893 (Roche *et al.*, 1986); further records of the plant in the next decade are from the surrounding areas. A recent study has reconstructed the most parsimonious invasion routes using a minimum cost arborescence algorithm (MCA; Hordijk & Broennimann, 2012) and revealed two separate invasions in North America, one starting from the east and the other from the west of the USA and Canada. The availability of a large amount of

ecological, distributional and cytological data and the presence of two independent invasions make spotted knapweed a useful unplanned, natural experiment to investigate how ecological and evolutionary factors might interact to result in the observed niche dynamics during biological invasions (Sax *et al.*, 2007).

Recent SDM studies have shown that the initial introduction of spotted knapweed in North America took place within climates similar to those in the native niche (Broennimann *et al.*, 2007; Broennimann & Guisan, 2008) but that the extent of the invasion could not be predicted when projecting models calibrated with the native range. This indicated that the species was able to invade areas with climatic conditions that differed from the native range, in particular into drier climates (Broennimann *et al.*, 2007; Treier *et al.*, 2009). The niche shift of spotted knapweed has been shown to be an exception among Holarctic plant invaders (Petitpierre *et al.*, 2012); it is therefore a particularly suitable model species for integrating a test for niche changes with a comprehensive and multidisciplinary approach that considers invasion routes and detailed knowledge of the species' biology. This integration is required to unravel the underlying evolutionary and ecological processes and to assess their importance at each phase of the plant invasion process.

Here, we present a novel approach to quantify niche changes through time along the two invasion routes and we interpret these findings in the light of known historical processes and experimental studies. We tested this framework using an extensive dataset of occurrences of spotted knapweed that covers the complete distribution of the species in Europe and North America, and we included comprehensive climatic data for these two ranges. For each species record, we gathered distributional, ecological and cytological information that was expected to correlate with mechanisms influencing niche changes at different phases of the invasion process. We also recorded whether the sample was collected in (semi-)natural or ruderal habitats (see Materials and Methods), because in its native range the tetraploid cytotype of spotted knapweed (i.e. the cytotype that colonized North America; Treier *et al.*, 2009) preferentially occurs in drier and more open microhabitats created by human-induced disturbances, while its diploid progenitor occupies (semi-)natural habitats with denser vegetation (Mráz *et al.*, 2012). These disturbances may have increased the likelihood that the plant was transported to a new range and facilitated the successful establishment of new populations and subsequent invasions (anthropogenically induced adaptation to invade theory; Hufbauer *et al.*, 2012).

Our main objective was to provide the first analysis of niche changes in space and time of a major plant invader, spotted knapweed, across its successive invasion stages in North America. More specifically, we asked the following questions. (1) Did climatic niche limits change through time during the course of the invasion and did they differ between the two invasion routes? (2) Did habitat types colonized by

the species change through time and did populations in (semi-)natural and ruderal habitats show different niche limits, and were these patterns different for the two invasion routes? (3) What can we learn about the observed patterns of niche dynamics in the light of historical, ecological and evolutionary processes evidenced in previous studies on this species? We present the results in relation to questions (1) and (2), and then discuss the results in the light of question (3).

MATERIALS AND METHODS

The species

Spotted knapweed occurs in its native range as a diploid and tetraploid cytotype but only the latter has been recorded in its invaded range (Treier *et al.*, 2009; Mráz *et al.*, 2011; Fig. 1). Such a pronounced shift in cytotype frequency has been explained either by stochastic founder events or by a superior establishment, colonization and persistence ability of tetraploids compared with diploids, since tetraploids are predominantly short-lived perennial polycarpic plants, while diploids are annual-biennial monocarps (Müller-Schärer *et al.*, 2004; Henery *et al.*, 2010; Hahn *et al.*, 2012).

Occurrence data

We began by updating the database for *Centaurea stoebe* (Asteraceae) in Europe and North America previously used in Broennimann *et al.* (2007) and Broennimann & Guisan (2008), mainly by expanding it to include data from Russia and eastern Europe as well as eastern North America. We meticulously searched local and regional herbaria and databases available online (see Appendix S1 in Supporting Information), revised herbarium vouchers in selected European herbaria (Appendix S1), included all available cyto-geographical data (P. Mráz *et al.*, unpublished data), and revised distributional data published by Ochsmann (2000). We only recorded occurrences for which ploidy level, habitat description and date of collection were available. When cytological data were not directly available for a specimen, we used scans of herbarium vouchers to ascribe the ploidy level based on morphological characteristics (Mráz *et al.*, 2011). Using these data, we created separate datasets for each of the four geo-cytotypes, the European diploid i.e. *C. stoebe* s. str., the European tetraploid, i.e. *C. stoebe* s. lat., the North American tetraploid from the east coast and the North American tetraploid from the west coast. North American populations were attributed to the east or west coast invasion according to the reconstruction of the invasion routes (Hordijk & Broennimann, 2012; see also Fig. 2). These datasets provide the most exhaustive historical and distributional information on spotted knapweed to date, with 3631 occurrences recorded between 1831 and 2010, with good coverage of the areas in which the species has been reported (Fig. 1).

Natural and ruderal habitats

The habitat information was classified according to the European classification system of habitats (EUNIS, 2008). Information gathered from herbaria, online databases or from our own sampling were carefully analysed, first using keywords from the habitat descriptions in EUNIS, then using Google Earth in cases of ambiguity or lack of information. The habitats belonging to the categories of diluvial sediments (C), natural and semi-natural grasslands (E) and natural rocky outcrops (H) were classified as (semi-)natural, whereas habitats belonging to agricultural habitats: fields, vineyards (I) and artificial and industrial habitats: transport networks, extractive industrial sites (J) were interpreted as ruderal habitats.

Climatic data

We used eight bioclimatic variables at 10' resolution derived from raw climatic data from the CRU CL 2.0 dataset (New *et al.*, 2002): ratio of actual and potential evapotranspiration (*aet/pet*); number of growing degree-days above 5 °C (*gdd*); annual precipitation (*p*); potential evapotranspiration (*pet*); number of months with drought (*ppi*); seasonality of precipitation (*stdp*); annual mean temperature (*t*); annual maximum temperature (t_{\max}); and annual minimum temperature (t_{\min}). The CRU CL 2.0 data covered 1961–1990, which was not the entire timeframe examined in the study, but it was considered that this bias would be negligible with regard to the amplitude of the climatic gradients covered by the species (e.g. c. 15 °C for annual mean temperature). The procedures for calculating *aet/pet*, *pet* and *gdd* from the raw CRU CL 2.0 data are detailed in Thuiller *et al.* (2005). The study area (the grey areas in Fig. 1) was selected to include all the biomes occupied by the species in Europe (EU) and North America (NA).

Statistical analyses

We performed a principal components analysis (PCA) on all the climatic variables covering all the sites in the study area using the `ADE4` library in R (Dray & Dufour, 2007). This produced an orthonormal system of principal components that maximized the environmental variation present in the study area. This method has been shown to be appropriate for quantifying niche overlap (Broennimann *et al.*, 2012). The first two axes accounted for 78.4% of the inertia of the PCA and corresponded broadly to a gradient of temperature and a gradient of humidity (see Appendix S2). Occurrences were then projected along the axes of this orthogonal environmental space. For each year and for each geo-cytotype, we considered all occurrences collected until that year and calculated the 2.5 and 97.5 percentiles of their scores along the two first axes as the lower and upper niche limits. This ensured that niche limits were defined by 95% of occurrences while the remaining 5% were considered to be outliers. Note that, with this

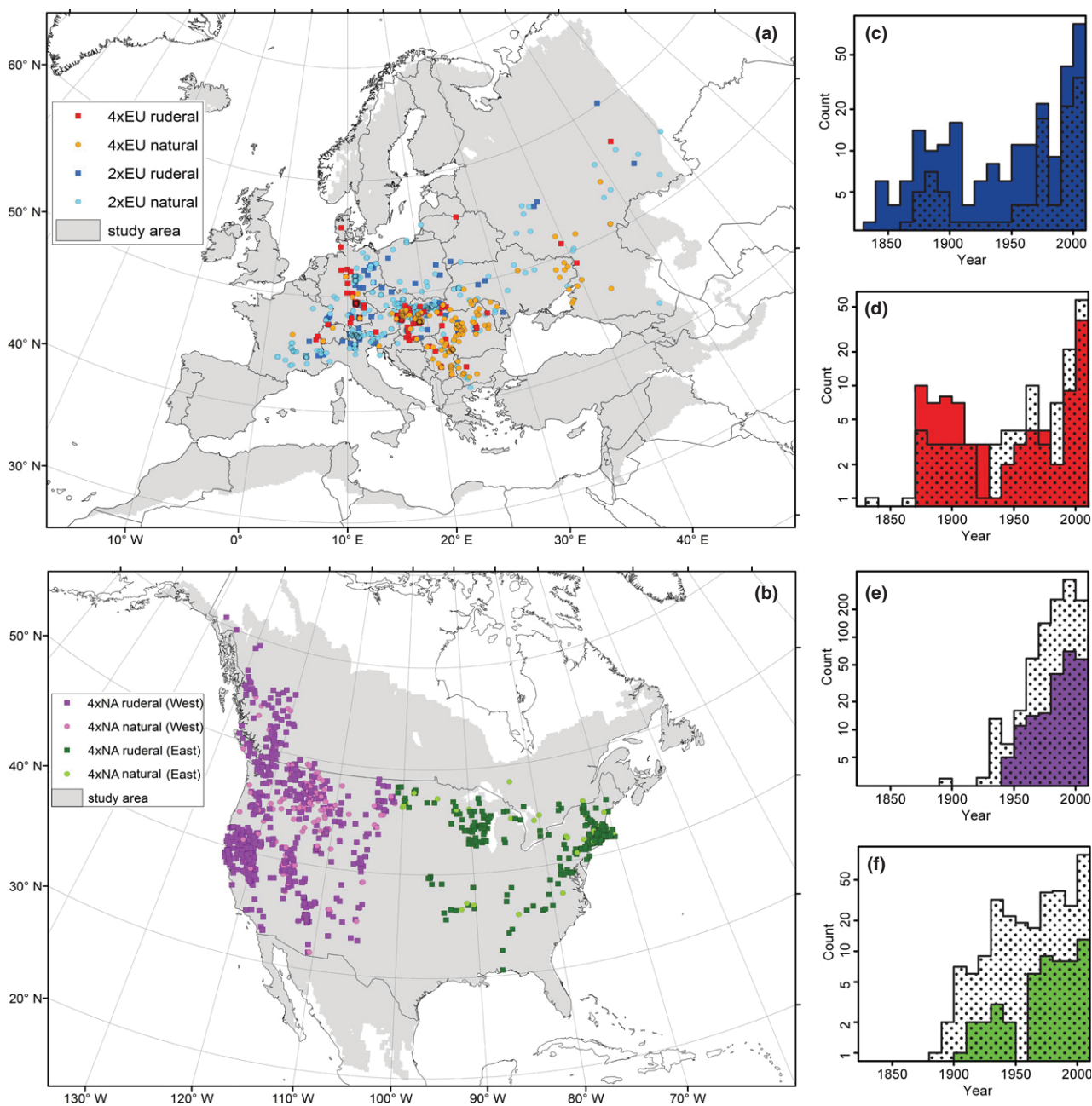


Figure 1 Occurrences of spotted knapweed (*Centaurea stoebe*) in its native European and introduced North American ranges. Spatial distributions of occurrences where dates of collection, ploidy level and description of habitat are known are shown for the native (a) and introduced (b) ranges. Populations found in (semi-)natural habitats are indicated with circles; those in ruderal habitats are indicated with squares. The number of occurrences in ruderal (dotted areas) and natural (solid areas) habitats per time slices of 10 years are shown for the European diploid geo-cytotype (2×EU) (c), the European tetraploid (4×EU) (d) and the North American tetraploid (4×NA) from the west coast (e) and east coast (f). Colours given in (a) and (b) correspond to those in (c–f).

procedure, we assumed that the species did not disappear from a site once colonized. This is a reasonable assumption for this highly invasive plant.

The niche limits were calculated only for years with more than five records. For each geo-cytotype, we performed non-parametric Wilcoxon tests to assess whether the niche limits were significantly different between populations growing in (semi-)natural and ruderal habitats. For each geo-cytotype,

we broadly defined a lag phase (i.e. the period of time between the first introduction and five populations), a spread phase (i.e. the period of time after the lag phase with only ruderal populations) and an expansion phase (i.e. the period of time after the initial phase with both ruderal and (semi-)natural populations) (Fig. 3).

Furthermore, we measured the climatic dissimilarity of each site of the study area compared with the native niche.

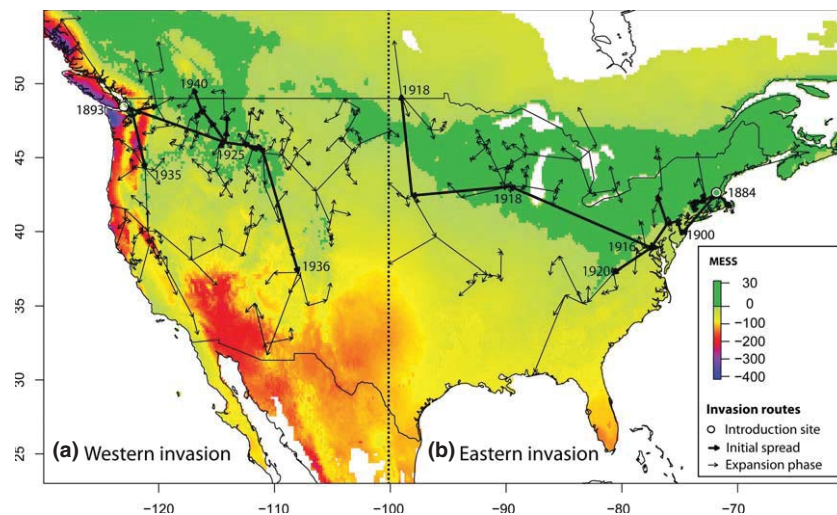


Figure 2 Pattern of spread and multivariate environmental similarity surface (MESS) analysis. A reconstruction of invasion routes originating from the western (a) and eastern (b) introduction sites is shown with arrows (from Hordijk & Broennimann, 2012). Thick and thin arrows correspond to the initial spread and expansion phases, respectively, as shown in Fig. 3. Dark green areas indicate sites with climatic conditions similar to those in the native niche (positive MESS values; note that both introduction sites are in green). The light green–blue gradient indicates the degree of dissimilarity with the climate of the native distribution (negative MESS values).

To do so, we computed multivariate environmental similarity surfaces (MESS; Elith *et al.*, 2010) using the library `DISMO` in R. The MESS analysis provided a representation of the similarity of grid cells (i.e. with the same resolution and extent as the climatic data) occupied by the species in the invaded range compared with the grid cells occupied by the species in the native range (thus defining the native niche), with respect to the set of environmental variables. A grid cell with a positive value indicated that it fell within the range of environmental values of the native niche, while a grid cell with a negative value indicated that at least one variable had a value that was outside the range of environmental values of the native niche.

RESULTS

Introductions to the new ranges and lag time

Both presumed introduction locations showed climatic conditions similar to those in the native niche (Fig. 3) and have been predicted to be suitable for the species by previous distribution models calibrated with native occurrences (Broennimann *et al.*, 2007; Broennimann & Guisan, 2008). The introduction in the west took place in slightly wetter conditions than in the native niche, according to the second axis of the PCA (Fig. 3d). Overall, however, our results, together with a number of other studies (Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Rödder *et al.*, 2009; Medley, 2010), provided evidence that sites of successful introductions matched conditions found within the native niche of the species. The MESS analysis also confirmed this because introduction sites showed positive values (Fig. 2).

Spotted knapweed did not spread immediately after being introduced into a new range. The distribution of the species remained confined to a few populations for about 20 years in the east, and about 40 years in the west (Fig. 3). In the west, the species remained restricted to the Victoria coastal area (British Columbia, Canada; Roche *et al.*, 1986), an isolated patch of wetter pacific climate surrounded by drier regions (Fig. 2a). This lag time is relatively short compared with most plants that have invaded temperate climates (i.e. Crooks, 2005; Daehler, 2009).

Initial spread in the introduced range

The initial spread and niche expansions of spotted knapweed in both the eastern and western invaded ranges were achieved almost exclusively in ruderal habitats (Fig. 3). Colonization of natural and semi-natural habitats started only after *c.* 30 years in the east (*c.* 10 years after the beginning of its spread in ruderal habitats) and after *c.* 60 years in the west (*c.* 20 years after the beginning of its spread in ruderal habitats) (Fig. 3). Most of the current eastern range of the species was already covered by the end of this initial spread phase, around 1920. In contrast, the initial invasion was much slower in the west, and only the north-western part of the range was occupied by the end of the 1950s, notably in Montana, USA, where several successive spread events occurred in the 1920s and 1930s (Fig. 2). Interestingly, the slow velocity of the invasion in the west matched the pattern of climatic distance from the native niche, reflecting the fact that it probably took more time for the species to establish in habitats that were quite different compared with the ones present at the introduction site (Fig. 2a). During this initial spread phase, niche limits in both ranges remained similar to

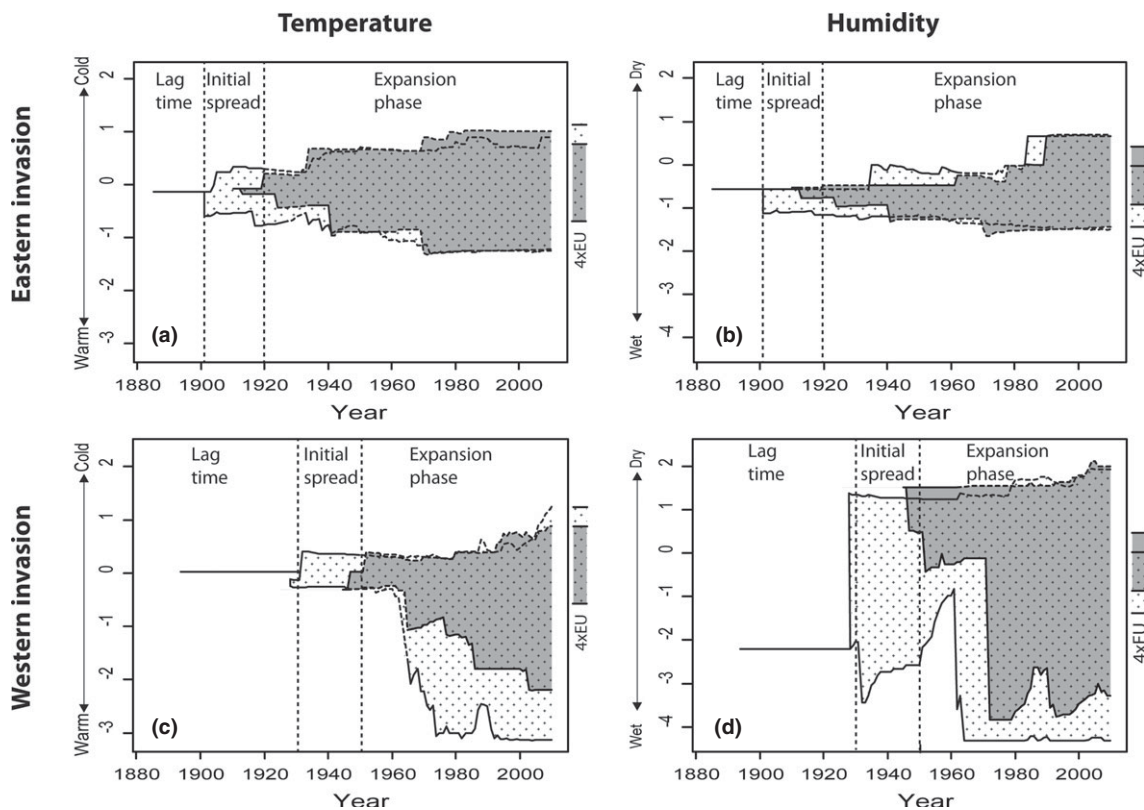


Figure 3 Dynamics of niche limits over time. The left panels show the change in the realized niche along a temperature gradient [first principal components analysis (PCA) axis, 56.3% of explained variance]; the right panels show the change in the niche along a humidity gradient (second PCA axis, 22.1% of explained variance). (a, b) The niche limits over time for the eastern North American tetraploid geo-cytotype (4×NA) populations; (c, d) the niche limits over time for the western 4×NA populations. Lines represent the 2.5% upper and lower quantiles. Solid and dashed lines indicate significant and non-significant differences, respectively, in niche limits between populations growing in natural (grey areas) and ruderal (dotted areas) habitats. Horizontal tick marks on the right side of the plots indicate the niche limits of the European tetraploid geo-cytotype (4×EU) for visual comparison.

those in the native niche, except for the humidity gradient in the western invasion, where drier habitats were suddenly colonized (i.e. mostly in Montana).

Main expansion and niche dynamics in the introduced range

Distinct niche limit patterns could be seen along the eastern and western routes. In the east, populations occupying (semi-)natural and ruderal habitats (Fig. 3a,b) gradually spread to colonize cold, dry and wet niche limits very similar to those of the European tetraploids, with only the warm niche limit being slightly altered compared with the native niche (Fig. 3a). This reflected the fact that new populations were able to establish in regions neighbouring those already colonized during the early spread phase or new regions with climatic conditions relatively similar to those in the introduction site (Fig. 2b). In contrast, the realized niche abruptly expanded in the western invasion, displacing the niche limits along the humidity gradient towards both ends, i.e. drier and wetter conditions (Fig. 3d), and then also gradually along the temperature gradient towards significantly warmer condi-

tions; the cold limit remained similar to that in the native niche (Fig. 3c). These niche limit expansions reflected the observed geographical spread after the 1950s towards the Dakotas (east USA), Colorado (south-east USA) and California (south USA), all of which provide different climatic conditions (Fig. 2a). During the last 30 years, the niche limits have not changed further.

DISCUSSION

Evidence of species' niche shifts during biological invasions are increasingly being reported (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Rödder *et al.*, 2009; Medley, 2010; Petitpierre *et al.*, 2012). However, Petitpierre *et al.* (2012) have shown that climatic niche shifts are actually rare among Holarctic plant invaders, but identified spotted knapweed as a remarkable outlier, confirming earlier findings by Broennimann *et al.* (2007). Unlike previous studies, here we have used novel temporal data and niche analyses to (1) reveal large expansions through time of the realized niche of spotted knapweed in its invaded range (Fig. 3), and (2) identify the time and mode of these niche expansions. This

temporally and spatially explicit dataset allowed us to show that different niche dynamics took place along distinct invasion routes in eastern and western North America. Below, we discuss the potential mechanisms and possible processes underlying the observed patterns of niche dynamics in the light of the historical, ecological and evolutionary processes found for this species.

Historical processes

The rapid spread of spotted knapweed on the east coast of North America, closely following the first known introduction record, was probably facilitated by the well-developed railroad network in the region (see the historical USA railroad map for 1890: Anonymous, 1951). This initial spread occurred mostly along linear transport corridors and ruderal habitats, as the colonization of natural and semi-natural habitats may have been impeded by the more competitive grassland species occurring in the eastern plains compared with the western habitats (Reinhart & Rinella, 2011). Furthermore, the spread may have been facilitated by the fact that the whole area covered by the eastern invasion is rather climatically uniform and similar to that in the introduction area and the native niche (Fig. 2; green area). Thus the species did not have to overcome significant climatic barriers to colonize the area, and hence did not require further adaptations to spread successfully.

The niche expansion characterizing the western invasion shows a remarkably different pattern. During a longer lag period, the species was confined to the Victoria coastal area (Roche *et al.*, 1986) (Figs 2a & 3c,d). The railroad network was far less developed than in the east during this period (Anonymous, 1951), making spread along transport corridors less likely. Without specific adaptation to the drier neighbouring conditions, the spread of the species outside the introduction area was probably more difficult in the west than in the east. The unintentional (probably propagules attached to undercarriages of vehicles; Sheley *et al.*, 1998) introduction to Montana around 1925 (Fig. 2) seems to have triggered its spread to most western states, which may explain the rapid expansion of all niche limits. The transition between the lag phase and the primary invasion phase occurred in the 1930–40s, with a dramatic expansion of the niche towards drier conditions, initially only in ruderal habitats. Interestingly, this rapid expansion of the niche coincided with the agricultural transition that followed the New Deal, which increased the productivity of USA agriculture by a factor of 10 and greatly modified the landscape and the environment (Conkin, 2008). These changes may have provided ample opportunities for spotted knapweed to invade open and disturbed habitats. This observed pattern suggests that human activities play an important role in driving invasion processes, by creating open niches and mediating the unintentional introduction and spread of propagules (D'Andrea *et al.*, 2009; Hufbauer *et al.*, 2012).

After about 120 years of invasion in North America, the niche limits of spotted knapweed seem to have reached a plateau for both the western and eastern invasions (Fig. 3). This suggests that the species has now colonized all types of potentially suitable climates in North America (but not necessarily all suitable places) and may thus be considered close to equilibrium with the environment. Note that the average range size of alien plants in Spain was shown to reach a maximum at 143 years (Gassó *et al.*, 2010). Equilibrium with the environment is an important assumption when applying SDMs (Guisan & Thuiller, 2005). If true, this result suggests that previous predictions of the potential range of spotted knapweed in North America should be considered robust when based on merged data from both the native and invasive ranges (Broennimann & Guisan, 2008) and would support the use of SDM predictions to guide the management of the species (e.g. Venette *et al.*, 2010).

Ecological processes behind niche dynamics: release from biotic constraints

Grasslands are sensitive to top-down controls (e.g. through herbivory) and exhibit rapid changes in plant composition when the intensity and frequency of those controls are altered (Seastedt & Pyšek, 2011). Escaping the strongly negative competitive effects of the neighbouring vegetation with which spotted knapweed co-evolved in the native European range (Callaway *et al.*, 2011) probably favoured its establishment and spread in the invaded range. Moreover, the large-scale overgrazing of North American grasslands that started during the agricultural transition in the 1930s may have reduced local competition by native plants and further favoured the establishment of the species. Indeed, it has been shown experimentally that the presence of dominant North American native grassland species significantly reduces germination rate, seedling survivorship, growth and densities of spotted knapweed (Rinella *et al.*, 2007; Knochel *et al.*, 2010; Emery & Rudgers, 2012).

Interestingly, the negative effect of competition is greater when spotted knapweed grows with native plant species from eastern grasslands than with native species from western grasslands (Reinhart & Rinella, 2011), suggesting a biogeographically dependent response to interspecific competition. The weaker effect of native western grassland species on the growth of spotted knapweed may result from the fact that spotted knapweed is better able to adjust its photosynthesis by its ability to uptake water deeper in the soil than native grassland species (Hill *et al.*, 2006). This could contribute to the observed spatio-temporal differences of spotted knapweed invasion between eastern and western North American grasslands.

Seven seed-head and four root herbivore invertebrate species have been introduced as biological control agents to limit the spread of spotted knapweed in North America (Müller-Schärer & Schroeder, 1993). Control programmes using seed-head herbivores have been quite successful, and

the loads of these herbivore species are now comparable in both ranges, but spotted knapweed has still largely escaped the effects of root herbivores (Blair *et al.*, 2008). In addition, laboratory feeding bioassays of generalist invertebrate herbivores from the native and introduced ranges of spotted knapweed have shown that the growth of North American generalist herbivores is far lower when fed on spotted knapweed than the growth of European generalists (Schaffner *et al.*, 2011). This suggests that biogeographical differences in the response of generalist herbivores to novel plant species may have further favoured spotted knapweed invasions.

Release from biotic constraints could have been a significant driver affecting the realized niche in the new range and contributing to the observed differences between the two invasion routes. Along the western route, the niche of spotted knapweed is remarkably larger than its native niche, with realized niche limits expanded towards warmer, drier and also wetter climates. Only the cold niche limits seem to have remained stable between the native and the western part of the invaded range.

Evolutionary processes behind niche dynamics: evidence for rapid post-introduction evolution

A recent comparative demographic study has shown a pronounced increase in growth rate from European to western North American tetraploids (Hahn *et al.*, 2012), consistent with the hypothesis and experimental evidence of rapid post-introduction evolution of spotted knapweed in the invaded range (Henery *et al.*, 2010). Release from both specialist and generalist herbivores (see above) is expected to result in the evolution of increased competitive ability (the EICA hypothesis, i.e. resources devoted to defence in the native range are reallocated to growth or reproduction; Blossey & Notzold, 1995). This expectation correlates well with the findings by Broz *et al.* (2009), which showed a reduced expression of gene transcripts related to constitutive defences in introduced populations of spotted knapweed compared with native tetraploids. This evolutionary change, probably achieved during the lag phase, might then have fuelled both the fast demographic spread in the introduced range and the ability of the species to colonize natural habitats with more competitive vegetation. Preliminary chloroplast DNA analyses of the populations used in our studies have revealed that the haplotypes present in North America are similar to the most common haplotypes in Europe (U.A. Treier, Aarhus University, unpublished results), excluding the possibility of an increased growth rate in North America as a result of the spread of a haplotype that is rare in the native range. Moreover, as previous studies have provided clear evidence for multiple introductions of spotted knapweed (e.g. Marrs *et al.*, 2008), rapid evolution may be more likely than genetic drift in explaining the observed evolutionary changes (Hahn *et al.*, 2012).

Another striking result of our analyses of niche limits is the conservation of the cold niche limits across the native and invaded ranges. This pattern mirrors experimental find-

ings for the invasive *Plantago lanceolata*, for which both native and introduced plants failed to set seed beyond the native elevational range margin and also shared a similar low-temperature limit to reproduction (Alexander *et al.*, 2012). More generally, this pattern fits the asymmetric abiotic stress limitation hypothesis (AASL), stating that species' distributions are primarily limited by physiological tolerance in the environmentally more stressful end of climatic gradients (Normand *et al.*, 2009). Stronger conservatism of the cold limit has recently been demonstrated for plant species with disjunct distributions in the Alps and the Arctic (Pellissier *et al.*, 2013). Several studies have shown that adaptations to cold climates are associated with massive reprogramming of gene expression (e.g. Survila *et al.*, 2010). Our results suggest that such adaptations have not happened in the invaded range, so that the species still occupies climatic conditions within its native fundamental (i.e. physiological) niche, but experiments are needed to substantiate this hypothesis further. Nevertheless, our study draws attention to the fact that some niche limits are more likely to be altered than others during biological invasions, depending on the prevalence of abiotic stress and competition as the main factors driving the distribution of the species (Normand *et al.*, 2009).

CONCLUSIONS

Evidence is accumulating that suggests that climatic niche shifts are occurring during biological invasions. To date, however, most studies have only assessed the overall niche change during invasions, using static approaches that compare current native and invaded ranges (e.g. Broennimann *et al.*, 2007; Fitzpatrick *et al.*, 2007; Rödder *et al.*, 2009; Medley, 2010; Petitpierre *et al.*, 2012) but do not take into account the spatio-temporal dynamics of the environmental niche along invasion routes, which is necessary to elucidate the potential mechanisms responsible for the observed changes. Our comprehensive dataset for spotted knapweed has allowed us to develop a novel approach that has revealed temporal niche dynamics along invasion routes. We have gone on to discuss these temporal patterns in the light of historical, ecological and evolutionary processes witnessed in previous studies for this species. Our results indicate that both the timing and the magnitude of ecological and evolutionary mechanisms that facilitate or prevent invasions may be intrinsically different between biogeographical regions (e.g. eastern versus western North America) and between opposite ends of ecological gradients (e.g. stressful versus competitive ends). Importantly, our study shows that detailed research on model alien invasive species, which includes both a multidisciplinary approach and a long-term commitment to data collection, offers a valuable complement to the many recent multispecies studies of niche changes during invasions. These findings significantly improve our understanding of biological invasions and may be used to direct future experimental studies to identify better the mechanisms responsible for the success of invasive species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of the herbaria and online databases used for collating the occurrences of spotted knapweed (*Centaurea stoebe*) in Europe and North America from 1831 to 2010.

Appendix S2 Eigenvectors (loadings) of the principal components analysis (PCA).

BIOSKETCH

Olivier Broennimann is a biogeographer interested in understanding the drivers of species' distributions under global change, in particular in the context of biological invasions. This study is part of his post-doctorate in the Guisan laboratory at the University of Lausanne.

Author contributions: O.B., A.G, P.M. and H.M.S designed the study; O.B. and P.M. collected the data; O.B. performed the analyses and drafted the manuscript; H.M.S. and P.M. strengthened the discussion on ecological and evolutionary factors; and A.G., H.M.S., P.M. and B.P. critically edited and improved the final version of the manuscript.

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