ORIGINAL ARTICLE

Climate change, anthropogenic disturbance and the northward range expansion of *Lactuca serriola* (Asteraceae)

Luigi D'Andrea[1]*, Olivier Broennimann[2], Gregor Kozlowski[3], Antoine Guisan[2], Xavier Morin[4], Julia Keller-Senften[1] and François Felber[1]

[1]*Laboratoire de Botanique évolutive, Institut de Biologie, Université de Neuchâtel, Neuchâtel, Switzerland,* [2]*Department of Ecology & Evolution, University of Lausanne, Lausanne, Switzerland,* [3]*Département Biologie, Université de Fribourg, Fribourg, Switzerland and* [4]*Centre d'Ecologie Fonctionnelle et Evolutive, Equipe BIOFLUX, CNRS, Montpellier Cedex, France*

ABSTRACT

Aim The distribution range of *Lactuca serriola*, a species native to the summer-dry mediterranean climate, has expanded northwards during the last 250 years. This paper assesses the influence of climate on the range expansion of this species and highlights the importance of anthropogenic disturbance to its spread.

Location Central and Northern Europe.

Methods Data on the geographic distribution of *L. serriola* were assembled through a literature search as well as through floristic and herbarium surveys. Maps of the spread of *L. serriola* in Central and Northern Europe were prepared based on herbarium data. The spread was assessed more precisely in Germany, Austria and Great Britain by pooling herbarium and literature data. We modelled the bioclimatic niche of the species using occurrence and climatic data covering the last century to generate projections of suitable habitats under the climatic conditions of five time periods. We tested whether the observed distribution of *L. serriola* could be explained for each time period, assuming that the climatic niche of the species was conserved across time.

Results The species has spread northwards since the beginning of the 19th century. We show that climate warming in Europe increased the number of sites suitable for the species at northern latitudes. Until the late 1970s, the distribution of the species corresponded to the climatically suitable sites available. For the last two decades, however, we could not show any significant relationship between the increase in suitable sites and the distributional range change of *L. serriola*. However, we highlight potential areas the species could spread to in the future (Great Britain, southern Scandinavia and the Swedish coast). It is predominantly non-climatic influences of global change that have contributed to its rapid spread.

Main conclusions The observation that colonizing species are not filling their climatically suitable range might imply that, potentially, other ruderal species could expand far beyond their current range. Our work highlights the importance of historical floristic and herbarium data for understanding the expansion of a species. Such historical distributional data can provide valuable information for those planning the management of contemporary environmental problems, such as species responses to environmental change.

*Correspondence: François Felber and Luigi D'Andrea, Laboratoire de Botanique évolutive, Institut de Biologie, Université de Neuchâtel, Rue Emile-Argand 11, 2009 Neuchâtel, Switzerland.
E-mail: luigi.dandrea@natucom.ch

INTRODUCTION

Lactuca serriola L. or prickly lettuce (Asteraceae) is a large winter or summer annual, west-euroasiatic species, which grows in meridional temperate climates (Lebeda *et al.*, 2004) but has been widely introduced in other regions (Carter & Prince, 1985; Zohary, 1991). Since the 18th century it has increased its geographical range towards northern Europe and now has a worldwide synanthropic distribution. The species belongs to a group of Mediterranean ruderal plants that have enlarged their distribution area during the last few centuries (Landolt, 2001).

Lactuca serriola is considered to be a drought-tolerant species (Werk & Ehleringer, 1986) and grows mainly in sunny microhabitats within anthropogenic habitats such as roadsides, railways, dumps and urban areas. It also occurs as a weed in a variety of crop fields where no-till or a conservation tillage system is used, such as in orchards, vineyards and pastures (Weaver & Downs, 2003; Lebeda *et al.*, 2004, 2007). It is a problematic weed in agricultural fields in Australia and North America (http://www.weed science.org/in.asp). The species is considered to be an 'r' strategist (Tilman, 1988), as its evolution has tended towards a short life cycle, strong self-fertilization ability, good adaptation for wind dispersal, quick germination and yellow flowers (Frietema de Vries, 1992; Mejias, 1993, 1994; Lebeda *et al.*, 2001).

The spread of *L. serriola* is closely related to human activities, mainly to increases in transport (Lebeda *et al.*, 2001) and changing patterns of land use. These processes have led to greater availability and better connectivity for disturbed and ruderal habitats favourable to *L. serriola*, such as wastelands, embankments, sides of ditches and roads, field margins and fallow fields (Feràkovà, 1977; Zohary, 1991; Lebeda *et al.*, 2001).

Global change, the components of which are linked to global industrialization and global trade, is a concept that brings together many environmental changes and subsequent ecological consequences. It includes the invasion of alien species into natural environments, biodiversity changes, climate changes, increased nitrogen deposition, and changing patterns of land use, often involving the destruction and fragmentation of natural habitats (Dukes & Mooney, 1999). Recently, concern about the impact of current climate change on organisms and the environment has increased greatly. Distributional latitudinal shifts have already been documented for many kinds of organisms (Walther *et al.*, 2002, 2005; Root *et al.*, 2003). It has also been demonstrated that climate warming can affect the dynamics of plant communities and influence the range expansion and contraction of species as well as their phenology and physiology (Davis & Shaw, 2001; Parmesan & Yohe, 2003). Root *et al.* (2005) showed recently that a significant portion of the changes observed in plant and animal traits can be attributed to increases in global temperature caused by human activity. However, correlations between climate changes and the distribution-range shifts of single species have been investigated mostly for small geographical areas (Kennedy, 1995; Pounds *et al.*, 1999; Sturm *et al.*, 2001; Johnstone & Chapin, 2003; but see also Walther *et al.*, 2005) or at upper elevation limits (Kullman, 2002; Penuelas & Boada, 2003).

Over the next century, increases in annual precipitation and temperature within the medium and high latitudes of the Northern Hemisphere and a global warming of 1.4–5.8°C are expected, depending on the particular climate-change scenario considered (Dukes & Mooney, 1999; IPCC, 2007). Since the end of the 19th century, the global temperature has increased by 0.6°C, on average; this figure is even higher if only landmasses are considered. From 1946 to 1975, temperatures decreased in the Mediterranean, Central Europe and Great Britain, whereas they continued to rise in Scandinavia and the rest of Europe. From 1976 to the present-day, temperatures increased rapidly across Europe, with the 1990s being the warmest decade of the 20th century (IPCC, 2007).

Improving our understanding of how climate and dispersal dynamics interact to drive migration rates is important for predicting future ecosystem responses to global change (Higgins *et al.*, 2003). It has been found that the geographical distribution limit of *L. serriola* in Great Britain corresponds to climatic variables related to the warmth and dryness of the summer (Prince *et al.*, 1985). This strongly suggests that climatic factors exert a dynamic control over the distribution limit of this species. For instance, temperature and photoperiod are two factors likely to control the time of blooming (Prince *et al.*, 1978). Moreover, seed germination is affected by climatic variables such as rainfall and temperature (Carter & Prince, 1985).

Seed production and germination are crucial factors in the colonization success of *L. serriola*. Using a population dynamics epidemic model, Carter & Prince (1981) simulated a small change in the production of seeds, showing that such a change was sufficient to modify the balance of colonization and extinction rates, and, therefore, to explain a sharp biogeographical range limit. We thus hypothesize that climate has contributed to variations in the geographic range of *L. serriola* in the past, indirectly through the environmental variables that affect its establishment and/or directly through traits such as flowering time or seed set production.

We focus here on describing the spread of *L. serriola* in Europe and on assessing the influence of climate on the distribution of the species, in the context of a period of increased human disturbance in European ecosystems. For this purpose, we compiled historical data from natural history collections as well as from the scientific literature, and related these data to the past and present climates (e.g. Walther *et al.*, 2005). No previous study has documented the spread of *L. serriola* in time and space or tested the hypothesis of a climatically induced distributional shift of *L. serriola* during the past few centuries in Europe,

MATERIALS AND METHODS

Species occurrence data

Data on the geographic distribution of *L. serriola* were assembled through a literature search as well as through floristic and herbarium surveys. A floristic investigation of literature from 25 European countries resulted in 1365 occurrence records for *L. serriola*. The literature survey focused mainly on Germany, Austria and Great Britain (975 occurrences, 71% of the dataset). In addition, 24 herbaria from 15 other European countries were screened, resulting in 1785 *L. serriola* herbarium sheets. The herbarium data were more equally distributed than the literature data amongst all European countries.

Within these herbarium and literature data, we searched for the geographical coordinates of *L. serriola* localities. Six categories of precision were used: (1) exact coordinates, (2) precision to 50 km, (3) precision to 100 km, (4) precision to 300 km, (5) precision to 500 km, and (6) precision to more than 500 km. On maps, only locations with coordinates of up to 100-km precision for the herbaria and up to 300-km precision for the literature were considered.

The indication of abundance (if present in the literature) was divided into six categories: ND, no data; A, absent; P, present without indication of abundance; R, very rare to scarce; S, scattered; and F, common to frequent. Herbaria sheets provided no information about abundance, and therefore only the 'P' abundance category was used.

Distribution data for *L. serriola*

Maps of the spread of *L. serriola* in Central and Northern Europe were prepared based on occurrences using all herbarium data. We divided Europe into a 50 km × 50 km grid for this purpose. We considered a square to be colonized if it contained at least one occurrence. It has been shown that *L. serriola* exhibits invasive behaviour (Cottet & Castella, 1891; Jaquet, 1930; Landolt, 2001; Purro & Kozlowski, 2003; Hooftman *et al.*, 2006) and easily colonizes disturbed areas; it has also been repeatedly observed that, at this scale, the species persists once established. Thus, the occurrences of *L. serriola* were added cumulatively to the sequence of maps. The southern limit of the study area is defined by the Pyrenees mountains, southern France and northern Italy; it is limited to the east by the borders of Austria, the Czech Republic, Germany and Scandinavia (Fig. 1). Six time periods were defined. The first time period was 1821–50, followed by five 30-year periods: 1851–80, 1881–1910, 1911–40, 1941–70 and 1971–2000.

As previously mentioned, we had sufficient occurrences (more than 50 *L. serriola* literature locality indications) that were well distributed over the time periods for three countries: Germany, Great Britain and Austria. To follow the spread of *L. serriola* in these countries more accurately, we divided the data according to administrative units (counties for Great Britain and 'Bundesländer' for Germany and Austria), abundance and six time periods. In order to balance the data between categories, the time periods used were different from those used to construct herbarium maps. The first time interval was between 1632 and 1800, followed by five 40-year periods: 1801–40, 1841–80, 1881–1920, 1921–60 and 1961–2000. The herbarium and floristic occurrences of *L. serriola* were plotted on maps (except for category A – absent).

Climate data

We used the CRU TS 2.0 data set (Climatic Research Unit, University of East Anglia, UK; http://www.cru.uea.ac.uk/~timm/grid/CRU_TS_2_0.html), which provides monthly means, maxima and minima for temperature as well as for precipitation from 1901 to 2000 for a 0.5° × 0.5° grid resolution (i.e. about 55 km × 55 km). These data were obtained by the interpolation of observed climate data from more than 20,000 weather stations all over the world (New *et al.*, 2000). We used a grid of 8566 points for Europe.

Using the same time slices as considered for species data, we calculated a set of eight climatic predictors comprising the mean sum of precipitation during the winter (December to February), spring (March to May), summer (June to August) and autumn (September to November), the mean temperature of the spring and summer, the mean number of months with a minimum temperature above 10°C (the temperature required for seed germination), and, finally, the mean number of months without frost.

Distribution modelling

To test the role of climate in the distributional shift, we split the species data set from the 20th century into five periods of 20 years (1901–20, 1921–40, 1941–60, 1961–80 and 1981–2000). Hereafter, these time slices are called the 1910, 1930, 1950, 1970 and 1990 time slices, respectively. Other time periods could not be tested because of the lack of climate data prior to 1900.

Species distribution models (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005) were fitted using species occurrences and associated climate data. Absence of the species was randomly sampled in areas where the plant has never been known to occur.

First, a generalized additive model (GAM) (Hastie & Tibshirani, 1987; Yee & Mitchell, 1991; Guisan *et al.*, 2002) was fitted in R (R Development Core Team, 2005) using all occurrences jointly (pooled occurrence data and their associated climate from the 5 different time periods) to determine the optimal climatic conditions for the species to grow. It was assumed that the climatic niche of the species was conserved across time.

Then GAMs were fitted following a *k*-fold cross-validation procedure (Hastie *et al.*, 2001). The dataset was divided into five independent partitions corresponding to each time slice. For each time slice, the partition of the time slice to be evaluated was excluded and the four remaining partitions were
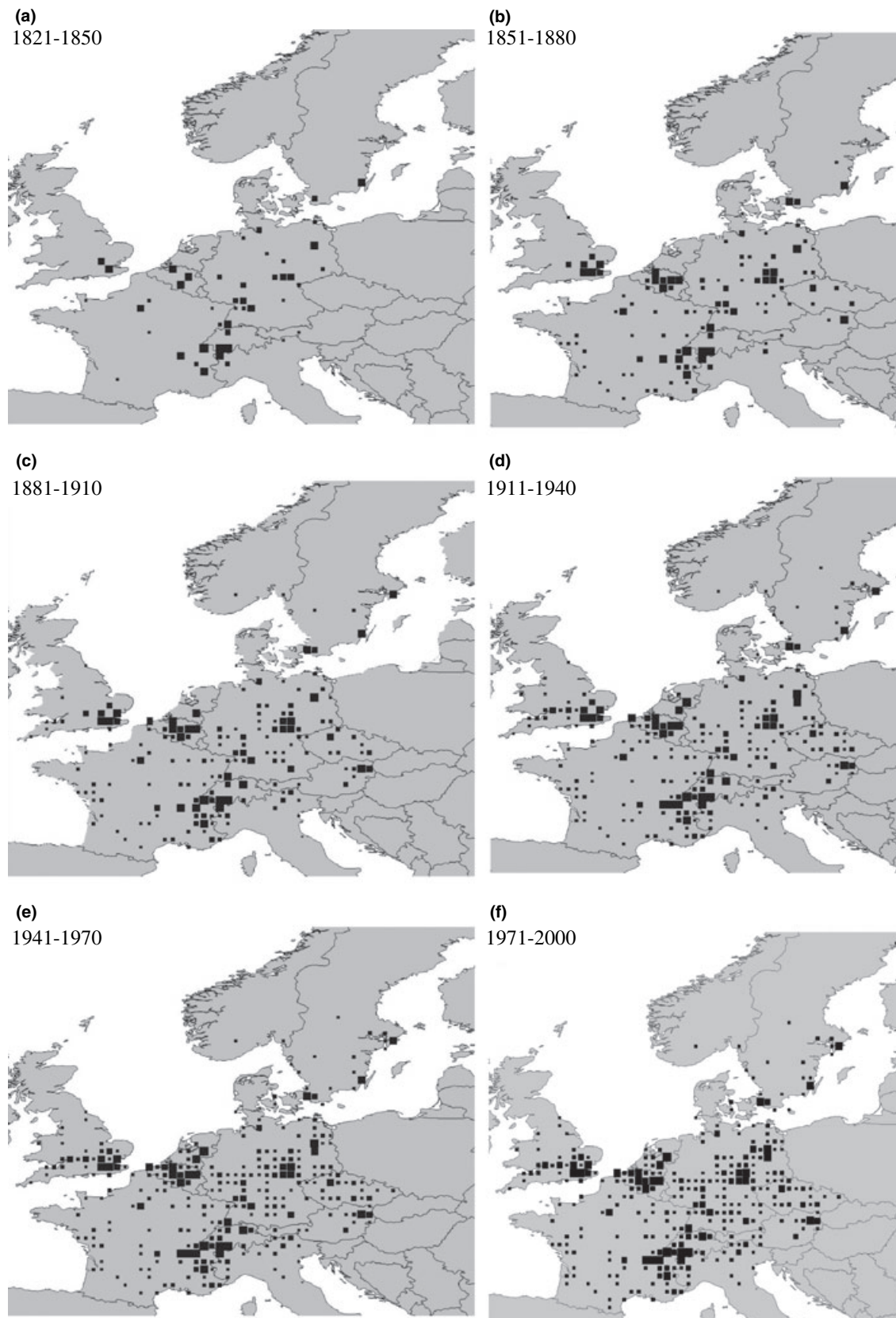
(a)
1821-1850

(b)
1851-1880

(c)
1881-1910

(d)
1911-1940

(e)
1941-1970

(f)
1971-2000

Figure 1 Distribution pattern of *Lactuca serriola* taken from herbarium data for (a) 1821–50, (b) 1851–80, (c) 1881–1910, (d) 1911–40, (e) 1941–70, and (f) 1971–2000. The square size increases with the number of occurrences.

used to calibrate the model. The model performance was then computed using the partition that had been eliminated (thus ensuring an independent validation measure of the model). This procedure was undertaken five times, for 1910, 1930, 1950, 1970 and 1990 time slices, respectively. Moreover, within each time-slice partition, the data were divided into 10 independent sub-partitions. This allowed for the calculation of 10 independent measures of the model performance for each time slice. Model performance was assessed through the calculation of the area under the curve (AUC) of a receiver operating characteristic (ROC) curve (Fielding & Bell, 1997; Pearce & Ferrier, 2000). AUC values indicate the correspondence between the predictions and the observations for the same time period. An AUC value of 1 means perfect agreement, an AUC of 0.5 means that predictions are not significantly different from random, and values between 0 and 0.5 mean that the model's predictions are worse than random. The following interpretation scale is typically used for ranking model predictions based on AUC (Swets, 1988): > 0.9 good, 0.7–0.9 useful, and < 0.7 poor. The calibrated models were then used to generate a projection of suitable habitats under the climatic conditions of each time slice.

RESULTS

Colonization of Europe from herbarium data

The changing distribution patterns are shown in Fig. 1. The maps show a northward spread of the species beginning in the early 19th century. Moreover, the results indicate that colonization in Great Britain and Scandinavia moved across the area from the south-east to the north-west.

The first occurrence of *L. serriola* in Europe, according to the herbarium survey, was reported in Belgium in 1765. Until 1820, few records of the species were available; *L. serriola* was present in Belgium as well as in southern France and Germany (not shown). In Switzerland, prickly lettuce had colonized the country and was found both north and south of the Alps. Interestingly, it was found at high altitudes as early as 1802 (e.g. Zermatt, 1620 m).

The species was collected for the first time in south-east England (Northfleet) in 1830 and in Sweden (Lund) in 1828 (Fig. 1a). Therefore, the first steps of the colonization of Great Britain and Scandinavia had already taken place at the beginning of the 19th century.

By 1850, *L. serriola* was widespread in Central Europe (France, Belgium and Germany) (Fig. 1a). From 1851 to 1880, the number of records increased in Central Europe, and the spread northwards continued: prickly lettuce was recorded on the north-eastern coast of England (Hartlepool, Cleveland). In Sweden, the species progressed from the coast of the Baltic Sea to Ostergötland (Fig. 1b) and colonized regions below 100 m. The next thirty years (1880 to 1910) were characterized by a westward spread: *L. serriola* progressed to the Norwegian border [herbarium record (HR) in 1903 in Langbro, Sweden] and had settled in the

centre of Norway (Bratsberg) by 1906. It colonized Wales, Cornwall and Devon in Great Britain (Fig. 1c), staying below 100 m and avoiding the Cambrian Mountains and the centre of the mainland.

The first herbarium record in Denmark (Copenhagen) is dated 1881, after Swedish colonization. The colonization of the Netherlands started at the very beginning of the 20th century, with the first herbarium sheet dated 1904. Prickly lettuce then colonized the centre of Great Britain, and the north-western coast of Wales and England through 1940; it also migrated above 100 m in Cirencester. In Sweden, *L. serriola* progressed northwards as shown in Fig. 1d, colonizing altitudes above 100 m. From 1941 to the end of the 20th century, the species progressed 700 km northwards along the Swedish coast (Fig. 1e,f).

Occasionally, herbarium sheets provided information about the dynamics of populations and the circumstances in which *L. serriola* arrived. A herbarium sheet from Besançon (France) dated 1874 noted that prickly lettuce had been 'abundant since the construction of the railway'. In a herbarium sheet from 1915 collected in Somerton (Great Britain), *L. serriola* was recorded as 'ballast alien'; in a 1922 sheet collected in Penrhyndeudraeth (Great Britain), it was recorded as 'adventive by railway'. In 1936, a sheet from Colchester observed: 'not noticed for some years, abundant for this year'.

Colonization of Austria, Germany and Great Britain from floristic and herbarium data

Because both types of data (floristic and herbarium) are used together, records coming from our herbarium survey will be annotated as HR.

Austria is of particular interest because of its orographic relief. However, only two items dating from before 1840 are available (Fig. 2b). One is the absence of *L. serriola* in the *Enumeratio Stirpium Plantarum quae sponte crescunt in agro Vindobonensi* of Jacquin (Jacquin, 1762) (Fig. 2a); the other is an HR of 1819 in Clausen (Tirol) (Fig. 2b). The mountainous region of the centre was colonized later. *Die Flora von Bad Aussee* (Rechinger, 1956) indicated the absence of prickly lettuce in 1956, whereas it is currently mentioned as rare (Fig. 2f).

Germany was rapidly colonized. The species is mentioned for the first time in the *Flora Halen* in 1761 (Leysser, 1761). The first HR was in 1819 in Plauen-Dresden. By 1800, *L. serriola* was found everywhere except in Saarland (south-west Germany), but its absence there was probably the result of a lack of data rather than of any real absence (Fig. 3a). From 1800, its abundance increased from the south to the north (Fig. 3b,c), until Germany was almost totally colonized by the beginning of the 20th century (Fig. 3d).

The distribution pattern of *L. serriola* in **Great Britain** is presented in Fig. 4. The oldest mention of *L. serriola* is a record from 1632 in the *Flora of Middlesex* in 1869 (Trimen, 1869). However, Prince & Carter (1977) stated that the general practice was to call unlobed-leaved plants *L. virosa*; therefore, they concluded that most pre-1930 records might as easily
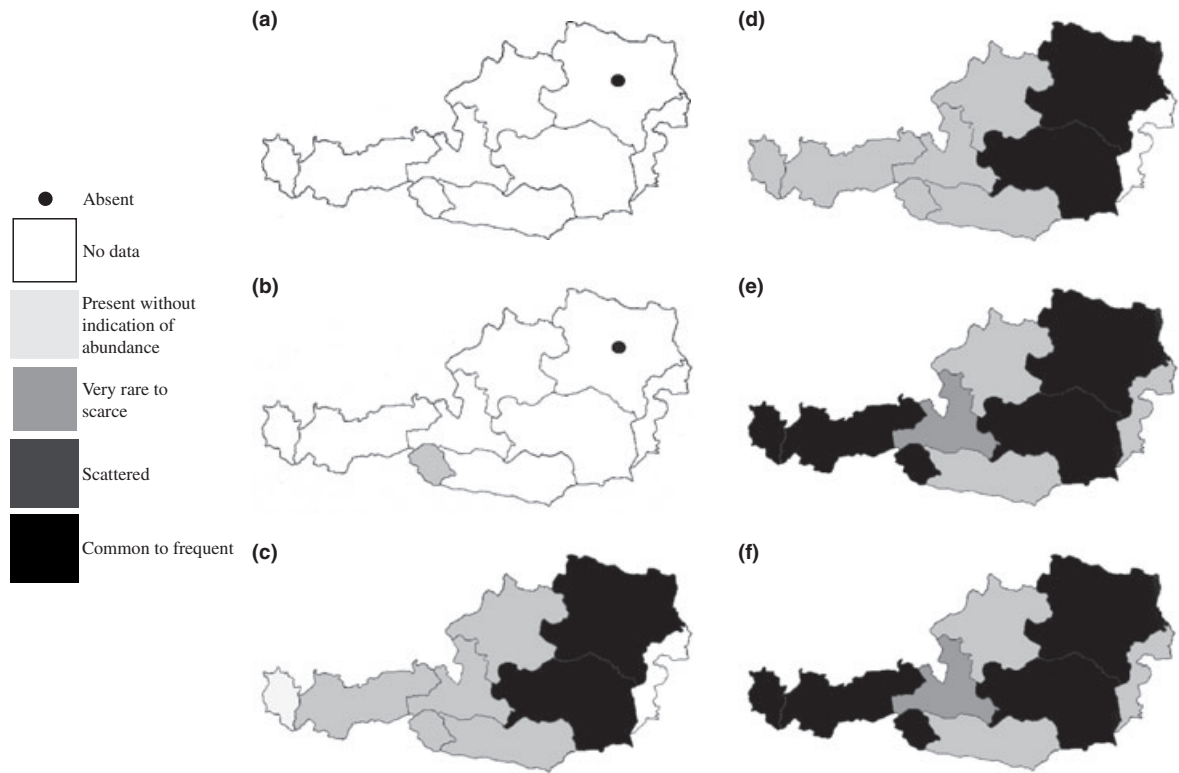
Figure 2 Distribution pattern of *Lactuca serriola* in Austria taken from literature data for (a) 1632–1800, (b) 1632–1840, (c) 1632–1880, (d) 1632–1920, (e) 1632–1960, and (f) 1632–2000.
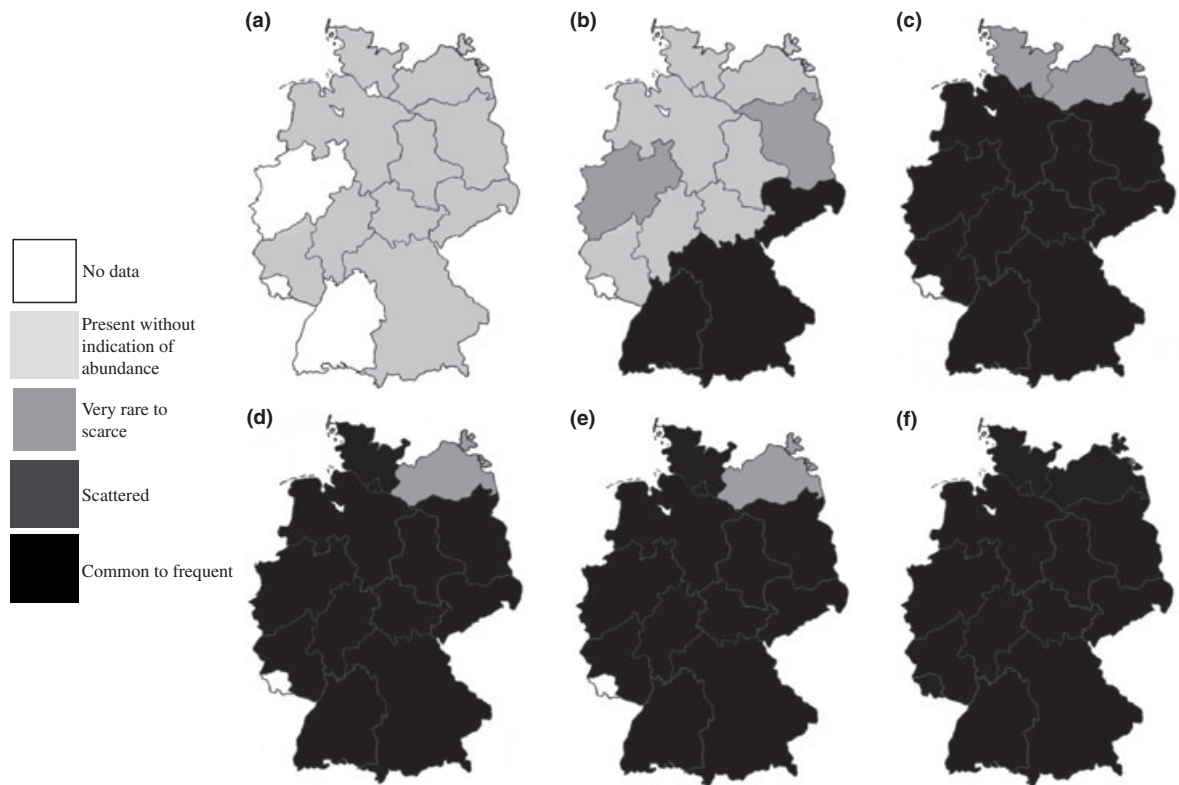

Figure 3 Distribution pattern of *Lactuca serriola* in Germany taken from literature data for (a) 1632–1800, (b) 1632–1840, (c) 1632–1880, (d) 1632–1920, (e) 1632–1960, and (f) 1632–2000.

Figure 4 Distribution pattern of *Lactuca serriola* in Great Britain taken from literature data for (a) 1632–1800, (b) 1632–1840, (c) 1632–1880, (d) 1632–1920, (e) 1632–1960, and (f) 1632–2000.

refer to *L. serriola* as to *L. virosa*. According to Oswald (2000, p. 156), 'the confusion occasioned by the failure of most British Floras of the nineteenth century to recognise that *L. serriola* can have simple leaves (…) has led to some uncertainties about the past status of this species and *L. virosa* in Cambridgeshire, as elsewhere in Britain'.

The expansion of *L. serriola* in Great Britain started from the south-east. In 1785, *L. serriola* was mentioned in the *Flora Cantabrigiensis* (Relhan, 1785) on the Isle of Ely (Fig. 4a). Until 1880, *L. serriola* remained confined to the south-east, spreading from the initial record location to reach Hartlepool (Cleveland) in 1866 (HR) (Fig. 4b).

Increasing numbers of records at the end of the 19th century indicate the colonization of eastern and north-eastern England (Fig. 4c). In 1889, the first HR for Wales (Bangor, Wrexham) was registered. In the *Flora of Glamorgan* (Wade, 1994), *L. serriola* is mentioned in Porthcawl in 1897. Then, in 1902 and 1907, prickly lettuce was recorded in Pembrokeshire and Cardiff, respectively. In 1901, *L. serriola* was mentioned as being scarce in the *Flora of Cornwall* (Davey, 1909), and an HR was registered in Par in 1908. It was collected along a railway bank near Newton Abbot (Devon) in 1909 (Fig. 4c).

At the beginning of the 20th century, prickly lettuce expanded to the western part of the mainland (Fig. 4d). Intriguingly, at this time, *L. serriola* was mentioned as being

absent from the flora of Wiltshire (Preston, 1888), Bourne-mouth (Linton, 1919) and Warwickshire (Bagnall, 1891). Thereafter, it colonized the southern and central parts of England and finally spread to Scotland, where the first record in *The Flora of Angus* (Ingram, 1981) appeared in 1967 (Fig. 4e,f).

After 1950, *L. serriola* increased in abundance in colonized areas, such as Warwickshire, where prickly lettuce was recorded for the first time in 1959 and the populations subsequently exploded (Bowra, 1992). Similar expansions are described for the Netherlands (Hooftman *et al.*, 2006) and Switzerland (Cottet & Castella, 1891; Jaquet, 1930; Landolt, 2001; Purro & Kozlowski, 2003), and probably occurred in many other countries.

Distribution modelling and climate-induced shift

The model using all occurrences retained seven out of eight environmental predictors, each of these statistically significant in explaining the distribution of the species. The model explained 56% of the variance of the data, indicating that meaningful climate predictors were incorporated in the model. The climatic conditions that were found to favour the presence of *L. serriola* in Europe were: temperatures in the spring of > 5°C, temperatures in the summer between 7°C and 15°C, 2–10 months of temperatures > 10°C, less than 300 mm of
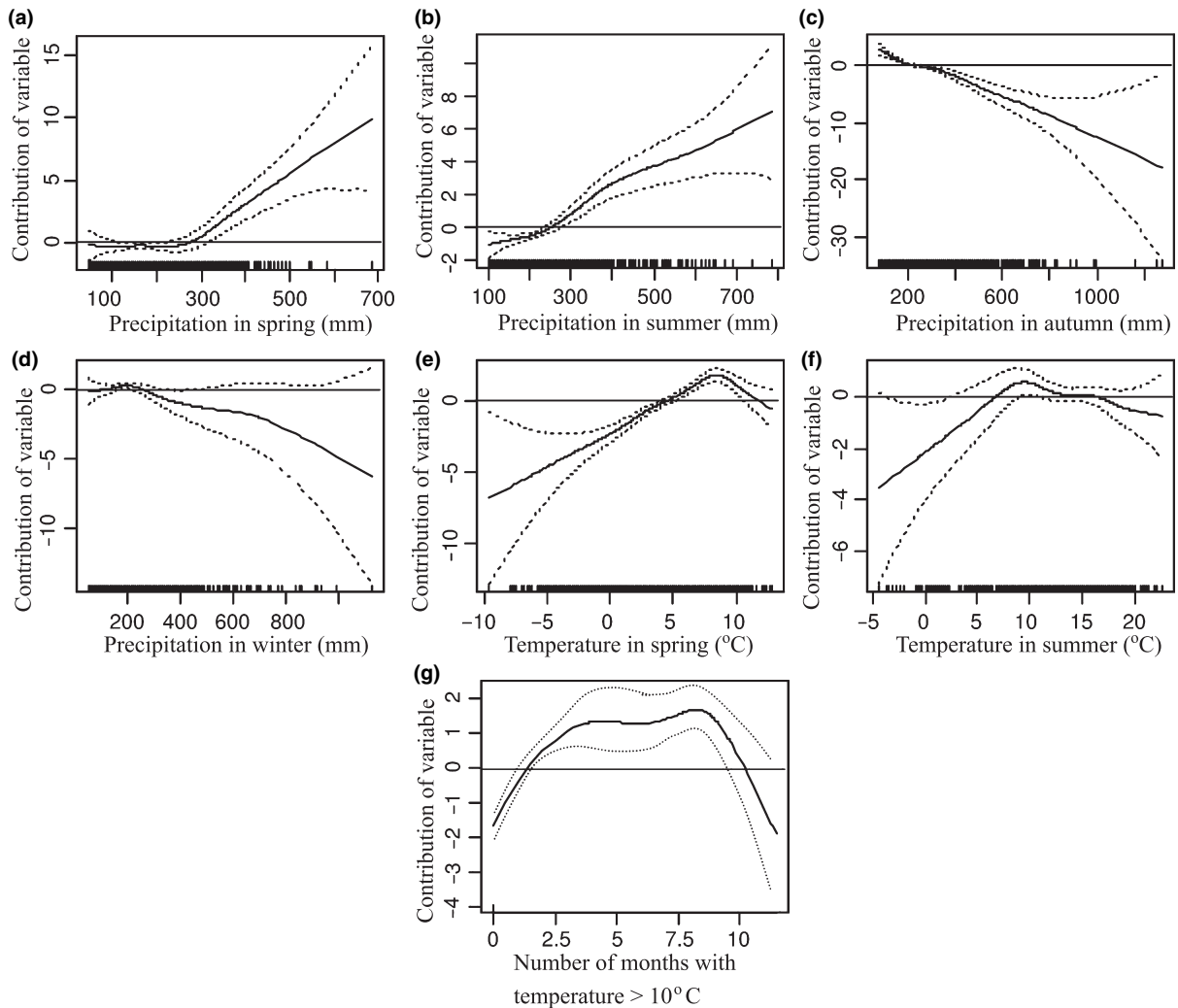
Figure 5 Response curves of the generalized additive models (GAMs). The *y*-axis shows the climatic suitability for *Lactuca serriola* (sum of additive terms + intercepts in the scale of the linear predictors, see Hastie & Tibshirani, 1987) along each climatic gradient. For each panel, the upper and lower standard error curves are shown by dashed lines and a rugplot is displayed along the base, showing the occurrence of *L. serriola* along the climatic gradient. The climatic suitability is shown for the amount of seasonal precipitation (a–d), the mean temperature in spring and summer (e–f) and the number of months with temperatures higher than 10°C (g).

rain in winter, more than 300 mm of rain in spring and summer, and less than 200 mm of rain in autumn (Fig. 5).

The results from the *k*-fold validation procedure illustrate the ability of *L. serriola* to track climate change during the last century. Figure 6a–e illustrates the predictions of areas suitable for colonization and the known occurrences for each time period. At the beginning of the 20th century, the species was predicted to have a high probability of presence in all of central Europe except the Mediterranean coast, the Aquitaine Atlantic coast, a large part of Scotland, and Scandinavia. Note, however, that the southern Swedish coast of the Baltic Sea had intermediate values of probability. In the subsequent time periods up until 1970, the suitable habitats for the species shifted slightly northwards, with areas in Scotland and southern Scandinavia becoming more

suitable (Fig. 6a–d). During the most recent time period, an enhanced northern distributional shift was predicted, with large parts of Scotland and Scandinavia becoming suitable (Fig. 6e); however, these new areas are not yet occupied by *L. serriola*.

The relationship between the potentially suitable areas and the actual occurrence of the species is further illustrated with AUC values on validation datasets (Fig. 6f). From 1910 to 1970, AUC values fell to between 0.85 and 0.90, indicating high levels of agreement between the predicted and observed data (Table 1). In 1990, however, the AUC value decreased to 0.47, indicating essentially random conformity between predicted and observed data. This is primarily as the result of the large areas in Sweden that were predicted to be suitable, but had not yet been colonized by the species.
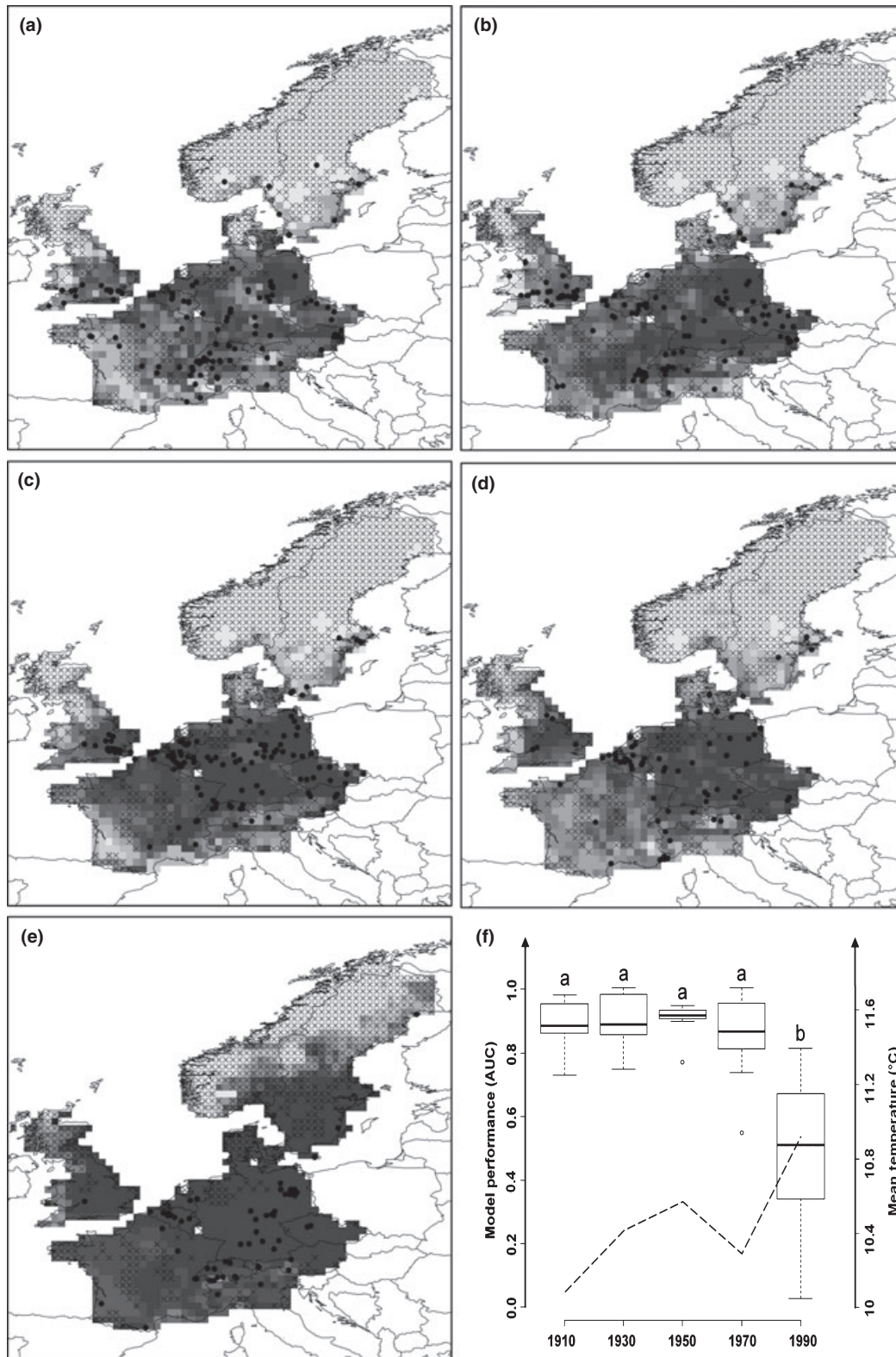
Figure 6 Climate-induced distributional shifts. Light and dark grey correspond to areas with low suitability and high suitability, respectively, for *Lactuca serriola*. Dots illustrate occurrences, and crosses correspond to absences (places where the species was never shown to occur). Maps (a–e) show the potential distribution of the species for the 1910, 1930, 1950, 1970 and 1990 time periods. Box-plots (f) show the agreement between potential distribution maps and actual occurrence data. The dashed line indicates the mean temperature in the study area for each time period. The rise of temperature in the last two decades coincides with the low level of agreement between known and potential distributions.

Table 1 Performance of the generalized additive models (GAMs) predicting the distribution of *Lactuca serriola* from climatic predictors for various time periods. The AUC calibration values correspond to the models' performances on the four data partitions used for calibration (not including the focal period). The evaluation values correspond to the models' performances on the remaining data partition. The values shown here correspond to the average of the AUC calculated for 10 sub-partitions.

Time slice	1910	1930	1950	1970	1990
Mean AUC calibration	0.979	0.983	0.979	0.983	0.981
Mean AUC validation	0.882	0.892	0.903	0.851	0.473

DISCUSSION

Using natural history collection data to quantify range change

For this study, it was hypothesized that the effects of climate change are already visible for prickly lettuce, and, in particular, that these effects caused the distribution of the species to shift towards the poles.

The use of herbarium specimens introduces several biases, including problems with identification of the plants in the field, the accessibility of the sampling sites, and the variability of the sampling effort over a long period of time. Some groups of species (e.g. aliens or garden escapes) were recorded less consistently (Delisle *et al.*, 2003), whereas other groups (rare, endangered or conspicuous species) were more frequently recorded. Nevertheless, our floristic and herbarium data revealed consistent trends: the colonization of Northern Europe by *L. serriola* happened at the end of the 18th century and during the first decades of the 19th century. At the same time, *L. serriola* increased its abundance in Central Europe. By the beginning of the 20th century, the species had colonized most of Europe. Locally, westward migration of the species was observed, from Sweden to Norway, southern England to Wales, Wales to Ireland (first record in 1996) (Preston *et al.*, 2002), and from the eastern part of Austria to the west. Our dataset does not allow us to draw any inferences about the colonization of the Iberian Peninsula, either from France or from North Africa. In Scandinavia, although the first steps of colonization took place in the south relatively early, the species is still not widespread. At present, the northern boundary of the distribution area runs near 66° N, through Sweden.

The colonization of lower altitudes and flat countries took place more rapidly than that of mountainous regions. Mountains are significant obstacles for plant migration, meaning that transportation from one valley to the next is more likely to take place by human intervention. In southern Europe, *L. serriola* has generally been observed at higher altitudes than in northern areas, although it has been collected at 680 m in Bratsberg, Norway. *Lactuca serriola* is now abundant in Central Europe (Lebeda *et al.*, 2001) and England (Bowra, 1992) and is still in a dynamic state of colonization. For instance, Hooftman *et al.* (2006) showed that *L. serriola* is spreading rapidly through the Netherlands. In Switzerland, the species was recorded as rare before 1900, but had totally colonized the country by the end of the 20th century.

A number of factors, such as global change (including climate change), increases in disturbances caused by the development of trade routes and urban areas, as well as the intensification of transportation, may have contributed to the spread of *L. serriola*. In the following section, we discuss how each factor might have influenced the distribution of prickly lettuce. Assessing their relative importance is difficult, as these factors may interact with each other.

Climate change

The only studies that have investigated the relationship between the distribution of *L. serriola* and climate were carried out in Great Britain. Prince & Carter (1985) concluded that the response to climate observed in *L. serriola* beyond its distribution limit was too small for the limit to be explained in terms of the failure of individual plants. In controlled environments, they found that the rate of development towards flowering was strongly related to temperature. Flowering was always faster within the distribution limit than beyond it, but no difference in fecundity was detected between the areas. Nevertheless, the authors stressed that, even if undetectable physiological responses slightly reduced the performance of the plant at the individual level, the secondary effects induced on the populations or the tertiary effects on the dynamics of metapopulations could be significant. Carter & Prince (1985) concluded that extremely subtle climatic changes are responsible for controlling *L. serriola*. For instance, mean temperature influences the rate of stem extension (Prince *et al.*, 1978), and hot, dry weather in the summer may favour the fruiting and/or the establishment of the plant in the following autumn. Even in the absence of any direct physiological effects, climate can have a significant effect on the persistence of *L. serriola*. For example, lower rainfall might lead to the maintenance of open habitats suitable for prickly lettuce. Thus, some aspects of the climate are likely to exert dynamic control over the distribution of prickly lettuce. Thus, when a year is climatically exceptional, *L. serriola* may extend its geographical and altitudinal ranges (Prince & Carter, 1985; Prince *et al.*, 1985). Climatic factors such as temperature, photoperiod and precipitation, which influence the environment and the establishment of the plant and/or its flowering and fruiting, may have a significant effect on the ability of individual plants to build viable populations and colonize new sites.

Modelling the distribution of the climatic niche of the species shows that, from the beginning of the 20th century to the late 1970s, the distribution of *L. serriola* corresponded to the climatically suitable sites available. This indicates that the species distribution range was in equilibrium with its climatic niche. The highest increase in temperature in the Northern Hemisphere during the last century actually occurred during the last two decades (Brohan *et al.*, 2006) and coincided with a sudden increase in areas predicted to be climatically suitable for *L. serriola*. However, we were not able to show a significant relationship between this increase and the known change in the species' distributional range towards northern latitudes. This may signify that climate changes are happening too fast for *L. serriola* to track. It suggests also that the range of the species could expand further in the future. Another interpretation of this discrepancy would be that a time-lag phase is necessary for the species to develop adaptive mutations or receive additional gene flow, or for migrants to overcome competitive constraints (Sakai *et al.*, 2001; Levin, 2003). Potential areas that might experience future range expansion are western Great Britain, Scotland, southern Scandinavia and the Swedish coast (Fig. 6e). An alternative explanation would be that the non-significant relationship found between climate change and dispersion in the last time series could be the result of an underestimation of the actual dispersion of the species. Botanists tend to collect more rare species. It is therefore probable that the sampling effort during the two last decades became less important in northern Europe as *L. serriola* became more abundant there.

The climate models predict a slight decrease in habitat suitability in the middle of the 20th century at the southern limit of the distribution (southern France). This decrease is not confirmed by current knowledge about the distribution of the species in this region. The decrease in habitat suitability is obviously a modelling artefact resulting from our failure to account for the entire distribution of the species when calibrating the model, as Spanish populations were not included in the analysis. If such southern populations had been taken into account, this region would probably have been situated in the middle of the response curve and would have been less affected by the climate shift.

Our models also did not correctly predict the presence of *L. serriola* in northern Scandinavia at the beginning of the 20th century. One possible explanation is that our resolution (50 km) did not permit the detection of all the favourable microsites for the species. Another explanation is that most of the herbarium sheets in Scandinavia were collected around urbanized centres, where temperatures are always higher than they are in the natural environment. Our model is generated using mean monthly climate values that cannot reflect short-lived climatic events or extreme conditions that may have an important influence on population dynamics (for example, a very hot and dry summer that affects the autumnal establishment of the plant).

Distribution limits can also extend without relation to the climate or biology in a climatically favourable zone. For instance, in epidemic models, the increase of susceptible sites near to, but beyond, a plant's distribution limit could displace its climatic equilibrium distribution limit without changes in the climate or in the biology (Carter & Prince, 1981). Thus, the availability and accessibility of colonizable habitats are also important factors for understanding the spread of a species. It is therefore of great importance to consider the interaction between landscape structure and climate change when trying to understand a plant's distribution limits in time and space.

Disturbance, habitat availability and dispersal

Non-climatic influences of global change, such as habitat modification, may dominate locally and are of great importance for the spread of species (Parmesan & Yohe, 2003). No data are available yet to quantify the impact of a disturbance on the population dynamics of *L. serriola*, but it has been noted that a population generally establishes within one year. Its persistence depends then on the continued availability of open areas uncolonized by plants in later stages of succession (Carter & Prince, 1985). The influence of disturbance on population expansion as well as on seed germination and establishment has already been shown for other ruderal plants (Bossard, 1991; Steinlein *et al.*, 1996). The expansion of *L. serriola* in anthropogenic urbanized ecosystems is discernable from occurrence data (Prince *et al.*, 1985; Bowra, 1992; Hill *et al.*, 2002; L. D'Andrea, personal observation) and from historical records.

The opportunity to be transported from one available habitat to another is a key factor for enabling colonization. As has already been stressed, the modern expansion of international traffic is likely to be accompanied by an expansion in the range of aggressive road-side weeds such as *L. serriola* (Clifford, 1959). These species should be the first to shift their ranges (Dukes & Mooney, 1999; Parendes & Jones, 2000; Landolt, 2001). In this context, Central and Northern Europe has witnessed a tremendous development in man-made habitats and transport networks during the past 250 years (the construction of motorways, railways, airports, canals and built-up areas, and increased agriculture), permitting *L. serriola* to expand rapidly. Indeed, roads and railways interconnect anthropogenic ecosystems and facilitate the expansion of plant species such as *L. serriola*, which possesses life-history traits that confer good colonization abilities and rapid generation turn-over (Forman & Alexander, 1998; Lebeda & Astley, 1999; Trombulak & Frissell, 2000; Dolezalovà *et al.*, 2001; Landolt, 2001; Hill *et al.*, 2002; Kowarik, 2003; Lebeda *et al.*, 2004). Roads and railways provide corridors along which the species can migrate (Parendes & Jones, 2000). Indeed, the seeds can be easily transported from one site to another through, for instance, the mud attached to cars and trucks and/or by the transportation of various materials over long distances (Pitelka *et al.*, 1997).

The occupation of new regions occurs through passive seed dispersal and the establishment of seedlings in sites where conditions are suitable (Davis & Shaw, 2001). However, the ability of species to migrate rapidly across large distances might

be driven primarily by infrequent long-distance dispersal events that are difficult to quantify (Higgins & Richardson, 1999; Malcolm *et al.*, 2002). Prince *et al.* (1985) underlined the importance of long-distance seed-dispersal events for building new *L. serriola* colonies, which is impossible to prove from our results. However, several first records of the species at short time intervals, but long distances from each other, could indicate that such events did happen.

Such long dispersal events could lead to the formation of outlier populations, exerting a continual outward pull (Cain *et al.*, 2000) and resulting in a more rapid migration than that along a single population front (rapid in-filling of the intervening space). However, outlier populations may fail to build viable populations, making the frequency of introduction and the number of seeds introduced beyond the distribution limit of great importance. In this context, the growth in the volume of trade along commercial routes greatly increases the frequency with which introductions are repeated (Perrings *et al.*, 2005). Moreover, the seed bank formed from 1 year can substitute for a lack of immigrant seeds the next year; one single plant of *L. serriola* can produce a huge number of wind-dispersed seeds and potentially form a short-term (1–3 years) seed bank (Weaver & Downs, 2003).

The dual influences of human habitat modification and anthropogenic climate change are likely to favour mobile species (Warren *et al.*, 2001); the combination of the two factors probably favoured the rapid spread of *L. serriola*.

CONCLUSIONS

Our results draw attention to the possible impact of components of global change, such as climate warming or habitat disturbance, on the expansion of ruderal Mediterranean plant species such as *L. serriola* towards northern regions in Europe. Our work highlights that such a ruderal plant species is currently not at equilibrium with its niche. Thus, potentially many species with a similar ecology could expand much further beyond their current range. Moreover, our paper exemplifies the importance of floristic and herbarium data for a global understanding of the spread of a species. Historical data can thus form the basis for detailed studies and for the management of modern environmental issues, such as assessing the influence of changing environmental factors on the response of a species, invasion or biodiversity changes. The validation of models through a comparison of observed range shifts with model predictions is a key step forwards in improving projections of climate change on species and their viability (IPCC, 2007). Finally, our study, using *L. serriola* as a model species for studying colonization routes in Europe, will help to better predict and manage future expansion of the species. These data could also serve as a basis for further molecular studies on the migration routes and genetic diversity of this species in Europe.

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BIOSKETCH

Luigi D'Andrea's research projects have focused on molecular and historical biogeography as well as on conservation biology. He is currently interested in environmental issues linked to GM crop cultivation and is expanding his interests in the agricultural–ecological–biological field of research as well as in fields such as ecological economics and agroecology.

Editor: Miguel Araújo