

Potential impact of climatic change on the distribution of forest herbs in Europe

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The aim of this study is to evaluate the possible consequences of climate change on a representative sample of forest herbs in Europe. A fuzzy climatic envelope was used to predict the location of suitable climatic conditions under two climatic change scenarios. Expected consequences in terms of lost and gained range size and shift in distribution for 26 forest herbs were estimated. These results were combined in an Index of Predicted Range Change for each species. Finally, the effects of habitat fragmentation for potential dispersal routes were evaluated and options for management on a European scale are discussed.

Generally, a good agreement of the estimated suitability under the present climate and the observed current distribution was observed. However, species vary a lot in the degree to which they occupy the presently climatically suitable areas in Europe. Many species are absent from large areas with suitable climate and thus could be said to have poor range-filling capacity.

A general change in location (range centroid) of the total suitable area was observed: The total suitable area will on average move strongly northwards and moderately eastwards under the relatively mild B1 scenario and more strongly so under the A2 scenario. The required average minimum migration rate per year to track the potential range shift is 2.1 km under the B1 scenario and 3.9 km under the A2 scenario.

Moderate losses in the total suitable area in Europe are predicted for most species under both scenarios. However, the predicted changes are very variable, with one species (*Actaea erythrocarpa*) experiencing total range elimination in Europe (A2 scenario) while the total suitable area is predicted to show large increases for other species. The species that are predicted to experience the greatest proportional losses in their climatically suitable area within their presently realised range tend to have northern or eastern range centroids.

The Index of Predicted Range Change roughly divides the species studied in four groups: One species face a high risk of extinction; eight species are expected to experience moderate to severe threat of extinction; 11 species are not considered at risk and, finally, six species may actually benefit from global warming.

An analysis of potential migration routes shows the importance of maintaining and, if possible, improving the network of forest throughout Europe to make migration possible. It is also suggested to closely monitor the status of boreal and subalpine species that are most threatened by global warming. Finally it is recommended that special concern should be given to increased protection and restoration of forest habitats in southern montane areas for their crucial long-term importance for the maintenance of European plant diversity.

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Major climatic changes are predicted for the coming century as a result of increasing atmospheric concentrations of greenhouse gases (Anon. 2001). Regional and seasonal climate patterns are expected to change as a result (e.g. Hulme et al. 2002, Sala et al. 2000). Generally, the climate is predicted to be warmer in the future with global average increases in temperature of 1.4–5.8°C (Anon. 2001). This warming will be accompanied by changing patterns of precipitation (Anon. 2001). Depending on the actual magnitude of climatic change such changes may severely affect the distribution of species and alter present-day vegetation composition and biodiversity patterns. The Earth's climate has already warmed by $0.6 \pm 0.2^\circ\text{C}$ over the 20th century (Anon. 2001) and the ecological consequences for a number of species have been documented (e.g. McCarty 2001, Parmesan et al. 1999, Walther 2000, Walther et al. 2002).

The possible consequences of climatic change pose serious challenges for the management of biodiversity (e.g. Williams et al. 2003). A plant species may, depending on its tolerances and dispersal capacity 1) stay and survive (if the climatic change is within its climatic envelope); 2) stay with slowly declining remnant populations (Eriksson 2000) in a sub-optimal environment and eventually go extinct; 3) track the changing climate (Pitelka et al. 1997). A fourth option, evolution, may have some importance in the longer term (Davis and Shaw 2001), but will probably be of limited scope due to evolutionary conservatism (Svenning 2003, Prinzing et al. 2001). Recently, a number of studies have called for a closer coupling between climate change models, projected shifts in biodiversity patterns and land-use patterns in order to provide better advice for proactive biodiversity management. (Hannah et al. 2002a,b Midgley et al. 2003, also cf. Higgins et al. 2003). In this paper we try to assess and quantify the likely impacts of climatic change for European forest herbs as an example of a group of organisms with low dispersal potential and very specific habitat requirements. It has been hypothesised that many forest herbs will be unable to maintain their present range of distribution under a changing climate due to dispersal limitation and habitat fragmentation (Honnay et al. 2002).

Recently, a number of studies have described possible effects of climatic change on the distribution of plants and animals (Huntley et al. 1995, Box et al. 1999, Baker et al. 2000, Crumpacker et al. 2001, Bakkenes et al. 2002, Berry et al. 2002). In most of these studies it is assumed that macroclimate is a major determinant of plant and animal distribution on a large geographical scale. However, it is clear that other factors may also be of importance, notably at smaller scales (Pearson and Dawson (2003) for a discussion). Examples of such factors are dispersal, soil properties, topography, competition, or other biotic interactions (Pakeman 2001,

Whittaker et al. 2001, Woodward and Beerling 1997). Nevertheless, it is generally accepted that climate is a major factor controlling the natural large-scale distribution of plants (e.g. Sakai and Weiser 1973, Shao and Halpin 1995, Huntley et al. 1995, Chuine and Beaubien 2001, Pearson and Dawson 2003, Pither 2003, Svenning 2003).

Given these considerations we applied a fuzzified (sensu Kosko 1994) climatic envelope to assess the potential range impacts of near-future changes for European forest herbs. The concept of climatic envelopes was partly included in the life zone system of Holdridge (1967) and was further developed by Box (1981) and applied to the global distribution of functional plant types. Since then, many other climatic envelope models have been proposed (see Guisan and Zimmermann (2000) for an overview). It is generally accepted that a climatic envelope should reflect aspects of temperature (energy requirements, heat/cold tolerance) and water balance (amount and timing of precipitation in relation to evapotranspiratory demands) (e.g. Sykes et al. 1996, Bakkenes et al. 2002). Theoretically, if a climatic envelope (niche) exists for a plant species and it is parameterised correctly, we will be able to predict where a given plant species will find its potential and optimal future distribution range.

Since the expected near-future climatic change is mainly human driven, the magnitude of change depends on how the global society succeeds in reducing the release of greenhouse gases mainly by lowering the burning of fossil fuels. Predicting future climatic scenarios relies on complex mathematical physically based climate models (Anon. 2001). Such models are still not perfect and cannot simulate all aspects of climate, but do nevertheless provide useful scenarios of future climate development. Various model predictions, however, are not in total agreement. This is caused by differences in model structure and complexity, imperfect knowledge about cause-effect relationships in atmospheric processes and uncertainty related to future global development trends. The Intergovernmental Panel on Climatic Change (Anon. 2001) has described a number of possible emission scenarios. These scenarios are used to parameterise climatic models. We have chosen to calculate the possible impact of two different scenarios, the B1 and A2 scenarios, respectively. The B1 scenario describes a world with a constant or gradually declining global population, but with rapid change toward a service and information economy, with reduced use of natural resources and the use of clean and resource-efficient technologies. The A2 scenario describes a heterogeneous world with a continuously increasing population. Economic development is primarily regionally and fragmented. It represents a business-as-usual scenario where release of greenhouse gases continues at their current rates or even increase (Anon. 2001). While a number of

global circulation models have been developed (Mitchell et al. (in press) for an overview), we used the HadCM3 global circulation model in the present study.

Based on the potential range impacts predicted by the climatic envelope modelling, we also evaluate the effects of habitat fragmentation for potential dispersal routes and discuss options for management on a European scale.

Methods

All spatial operations and modelling were carried out using the desktop ArcGIS 8.3 and its extension Spatial Analyst (ESRI <www.esri.com>). The resolution of the analysis is 10' and the extent of the study is 11°W, 34°N to 32°E, 72°N (a total grid size of 380 × 430 pixels)

Selected species and distribution data

In this study, we focus on 26 species of forest herbs (see Table 2). These species were selected to represent a wide spectrum of range sizes and range locations. We believe the selected species together have distributions patterns qualitatively representative of the majority of European forest herb species. However, given the non-random species selection our focus in the analyses is on range and variability of the observed and predicted distributions, using means purely to summarize results across our 26 study species and not as quantitative estimates for the European forest herb flora as a whole.

Forest herbs were defined as species more or less restricted to forested environments, following Flora Europaea (Anon. 1964–1993) and Polunin (1969). Information on each species' current distribution was drawn from Atlas Florae Europaeae (AFE, Jalas and Suominen 1972–1994). This project has published presence-absence maps showing the distribution of >3000 species of higher plants in Europe (see also <http://www.fmnh.helsinki.fi/map/afe/E_afe.htm>). For each species, we only recorded it as present in areas where the species was recorded as occurring naturally, but discounted other areas, e.g. where it occurs as an established alien (i.e. naturalised), only occurred in the past, or where the status of the species is uncertain. However, we used the naturalised ranges in an informal validation of the fuzzy climatic envelope model. The AFE-project uses an equal-area mapping unit of 50 × 50 km based on the Universal Transverse Mercator (UTM) projection and the Military Grid Reference System (MGRS). These mapping units will be referred to as AFE cells in the following. There are gaps in the dataset due to uneven sampling effort, especially in Russia (which is not included in the present study), but it gives a reasonable assessment of the distribution of the plant species treated

(Bakkenes et al. 2002). From here on, we simply refer to our total study area (the land areas between 34°N and 72°N and 11°E and 32°E, excluding North Africa and Asia Minor) as Europe.

Bioclimatic variables

Three bioclimatic variables were chosen for this study: Growing Degree Days (GDD), absolute minimum temperature, and water balance. These variables represent heat requirements, cold tolerance and moisture requirements, respectively. The variables are all calculated from datasets based on monthly values of mean temperature and monthly values of precipitation. These datasets were provided for the current climate (1961–1990) as well as projected values for 2070–99 relative to the current climate for scenarios B1 and A2 as grids in a 10' spatial resolution by the Hadley Centre for Climate Prediction and Research (<www.metu.gov.uk/research/hadleycentre>) and The Tyndall Centre for Climate Change Research (<www.tyndall.ac.uk>).

Growing Degree Days – heat requirements

The length of the growing season and the influx of solar energy are captured by the index of Growing Degree Days (Prentice et al. 1992, Beerling et al. 1995, Pearson et al. 2002):

$$\text{GDD} = \sum \max\{0, (T_m - T_t)\},$$

where T_m is the mean daily temperature (interpolated from monthly averages) and T_t is a threshold value indicating the lowest growth temperature. A T_t of 5°C is used in accordance with most studies and is considered suitable for temperate climates (see above).

Absolute minimum temperature – cold tolerance

Low temperatures affect the survival of plants and may result in frost kill (e.g. Sakai and Weiser 1973, Prentice et al. 1992, Prentice 1993, Pearson et al. 2002, Pither 2003). The theoretical absolute minimum temperature of the coldest month (T_c) is calculated according to the following regression based on observations from a large number of climate stations (Prentice et al. 1992):

$$T_{\min} = 0.006 T_c^2 + 1.316 T_c - 2.19.$$

Water balance – moisture requirements

Precipitation alone is not a good measure of moisture available for plant growth and it is necessary to relate

precipitation to energy to get a useful index of moisture (Lenihan and Neilson 1993). In this study we use water balance calculated as the monthly difference between precipitation and potential evapotranspiration. The value is calculated per month and then summed per year. The potential evapotranspiration is calculated as:

$$\text{PET} = 58.93 \times T_{(\text{above } 0^\circ\text{C})}/12,$$

following (Holdridge 1967, Lugo et al. 1999).

This is a very simple index that requires only monthly average values of temperature and precipitation. Many authors, however, argue that the water retention capacity of the soil is very important when modelling plant distributions (summarised by Stephenson 1998). Many of these studies include this water holding capacity in the equation (often referred to as the 'simple bucket model'). In this study, we choose not to include soils in the model, mainly because the grain of the study (ca 50×50 km for the floristic data) is beyond the characteristic scale domain of edaphic variation (Pearson and Dawson 2003), in particular with respect to soil hydrology. Even within a generally unsuitable cell small pockets of suitable soil may exist and thus permit the occurrence of a plant species.

A fuzzy climatic envelope

In this study we used a modified version of the standard rectilinear climatic envelope (Guisan and Zimmermann 2000). The main features of the fuzzy climatic envelope are shown in Fig. 1. It is well known that the rectilinear model tends to overestimate the potential climatic space because outliers are included in the definition of the envelope (Carpenter et al. 1993, Guisan and Zimmermann 2000, Farber and Kadmon 2003). It is customary to avoid this by excluding 2.5% or 5% of the observa-

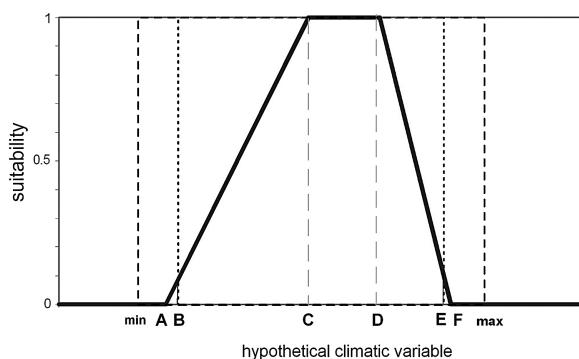


Fig. 1. A graphical representation of the fuzzy climatic envelope used in this study. In comparison, the outer vertical hatched lines (from min to max) represent the full rectilinear climatic envelope and the inner ones (from B to E) show the rectilinear envelope when outliers are removed. $B = 0.025$ percentile; $E = 0.975$ percentile; $C = 0.25$ percentile; $D = 0.75$ percentile; $A = B - 10\%(C-B)$; $F = E + 10\%(E-D)$.

tions in both ends of the spectrum to prevent the effect of outliers (Guisan and Zimmermann 2000). By doing so, however, it is easy also to remove valid observations and thus risk underestimating the true size of the envelope. This issue is particularly pertinent to climate change studies as it would lead to an exaggeration of the potential impact on species distributions. Another objection is the counter-intuitive nature of the binary model in relation to niche and gradient theories where species show an optimum response along a gradient (Austin 2002). Fuzzy sets provide a means for emulating environmental gradients without sharp borders (Center and Verma 1998). The fuzzy model is a continuum from 0 to 1 that represents the degree to which a given cell belongs to the envelope in regard to a given climatic variable. Most rectilinear models, on the other hand, apply a simple binary response of 0 or 1 (but cf. Sykes et al. 1996).

Figure 1 shows how we constructed the fuzzy envelope based on a set of observations. The figure also includes the full rectilinear climatic envelope with and without removal of outliers for comparison. The full fuzzy envelope based on all three climatic parameters is calculated as the degree to which a cell belongs to all individual envelopes (AND-ness). This is calculated as: minimum {variable 1, variable 2, ..., variable n} (Kosko 1994).

When designing the model structure, one of our main concerns was to make the model conservative with respect to the estimated climate change impact. Hence we chose to model species range limits according to a limited set of bioclimatic parameters, which are known to be of paramount importance as determinants of large-scale plant distributions (e.g. Sykes et al. 1996, Thompson et al. 1999, and Pearson and Dawson 2003). We chose to model the species tolerances to these bioclimatic parameters as simple, non-interactive thresholds to avoid the risk of overfitting the climatic relationships, which would cause the model to exaggerate the potential range shifts imposed by climate change. As an illustration of this point, we note that bioclimatic modelling of the distribution of *Taxus baccata* L. using artificial neural network modelling (Pearson and Dawson 2003) appears to underestimate the climatically suitable range (as indicated by native or naturalised populations) for this species in the British Isles (Thomas and Polwart 2003) and in Denmark (Hansen 1984), while the model using threshold limits in Sykes et al. (1996) provides a better fit.

Parameterisation of the climatic envelope

In order to define the climatic envelope for each species, we had to relate environmental variables on a $10'$ grid to species distribution data on a 50×50 km grid. The

number of pixels within each AFE cell depends on the amount of land present in the cell and generally increases with increasing latitude. The average number of pixels per cell is 29.6 (range: 1–74). For each bioclimatic variable we computed the mean value of all 10' grid pixels within the AFE cell boundaries. For each species all AFE cells with a record of natural occurrence were selected and the percentiles described above were calculated. The potential future distribution was calculated using the same methodology but replacing bioclimatic variables based on observed data with data generated by the HadCM3 model for scenarios B1 and A2, respectively.

Analyses of maps

For all maps (current potential distribution and potential distribution under the two climatic scenarios) we recorded (a pixel refers to a 10' × 10' grid cell): 1) overall suitability within current distribution range and in total (calculated as the sum of suitability for all cells within the current range and across Europe. 2) number of suitable pixels: number of pixels with a value > 0 (i.e. completely inside the envelope). 3) centre of gravity, i.e. the suitability weighted potential range centroid. 4) r/p ratio, the ratio between total overall suitability within the current distribution range (realised suitability) and the total overall suitability (potential suitability) – this measure theoretically equals one if a species is not limited by dispersal constraints (Gaston 2003).

These numbers were then used to calculate net change in suitability for two climate change scenarios across Europe, within the current distribution range and within current refugial range (see below). Table 1 summarises the results.

We also devised an index to describe potential net range size consequences of climatic change on the individual species (IoPRC = index of predicted range change). The fate of a species largely depends on (A) the change in suitability (under a given climate change scenario) within the current distribution range; and (B) the amount of new suitable climate space outside the current distribution range. A and B are given as ratios, with the predicted future suitabilities as proportions of the total current suitability for a given species. Furthermore, the importance of B depends on the species' ability to fill its climatic niche through migration and was therefore modified using the r/p-ratio as a proxy for dispersal capacity. Hence, the index is formulated as (see also caption to Table 2):

$$\text{IoPRC} = A + B \times r/p \text{ ratio.}$$

The index has values in the interval [−1, ∞]. A value of −1 indicates total loss of suitable space in Europe; values close to zero indicate status quo, either because suitable areas within the current distribution range are maintained or because new suitable territory outside the current distribution range alleviate losses within; values > 0 indicate that the species might benefit from the projected climatic changes.

Table 1. Predicted changes in climatic suitability (A) across Europe, (B) within current distribution range in all of Europe, (C) or just in the southern refugial region, as represented by (i) total suitability, i.e. the sum of the fuzzy suitability values, (ii) the total number of suitable pixels (with fuzzy suitability > 0).

	Scenario	Average	Min.	Max.
A. Across Europe				
Total suitability	Now*	0.236	0.003	0.400
	ΔB1†	−0.257	−0.610	0.503
	ΔA2†	−0.222	−1.000	0.790
Total no. of suitable pixels	Now*	0.433	0.006	0.694
	ΔB1†	−0.211	−0.926	0.318
	ΔA2†	−0.168	−1.000	0.659
B. Within current distribution range				
Total suitability	Now*	0.538	0.067	0.657
	ΔB1†	−0.387	−0.987	1.288
	ΔA2†	−0.541	−1.000	1.247
Total no. of suitable pixels	Now*	0.831	0.174	0.934
	ΔB1†	−0.345	−0.973	0.429
	ΔA2†	−0.480	−1.000	0.333
C. Within current refugial range‡				
Total suitability	Now*	0.438	0.067	0.588
	ΔB1†	−0.494	−0.902	1.289‡
	ΔA2†	−0.644	−0.996	1.246‡
Total no. of suitable pixels	Now*	0.745	0.174	0.893
	ΔB1†	−0.480	−0.848	0.429
	ΔA2†	−0.619	−0.999	0.333

*proportion of possible maximum value. † $\Delta x = (X - \text{Now})/\text{Now}$. ‡Excluding *Actaea erythrocarpa*, which is absent from the southern refugial area.

Table 2. Current range characteristics and predicted responses to climatic change under scenarios A1 and A2 for 26 European forest herb species: Longitude (long) and latitude (lat) of their current range centroids (in °); the ratio between realised and potential suitability (r/p ratio); the summed current suitability within the present range relative to that throughout Europe; the predicted suitability change (loss or gain) in year 2100 within the present range {suit-in} or the predicted, suitability in 2100 outside the current range (suit-new); both in proportion of the current suitability within the present range; and the Index of Predicted Range Change (IoPRC = 'suit-in' + [r/p ratio * 'suit-new']). IoPRC takes values interval [-1, ∞] with negative values indicating loss of suitable space in Europe and positive values indicating the species most likely to benefit from the projected climatic changes (see Methods). Potential migration distances: the distance in kilometers of the current positive range centroid {Mig-CC} or the smallest distance in kilometers from the current range margin (Mig-MC) to the centroid of the potential distribution in 2100 under a given climate scenario.

SCENARIO B1		SCENARIO A2													
Species		long	lat	r/p ratio	suit-in	suit-new	IoPRC	mig-CC	mig-MC	suit-in	suit-new	IoPRC	mig-CC	mig-MC	
<i>Actaea erythrocarpa</i>	25.64	66.33	0.604	-0.971	-0.014	-0.962	240	0	<i>Actaea erythrocarpa</i>	-1.000	0.000	-1.000	n.a.	n.g.	
<i>Cimicifuga europaea</i>	23.03	50.55	0.492	-0.987	1.199	-0.397	960	818	<i>Equisetum sylvaticum</i>	-0.468	-0.046	-0.430	1080	0	
<i>Equisetum sylvaticum</i>	17.37	55.25	0.853	-0.364	0.050	-0.321	836	0	<i>Cimicifuga europaea</i>	0.999	1.165	-0.426	1360	1115	
<i>Stellaria holostea</i>	12.18	49.65	0.894	-0.391	0.207	-0.206	576	0	<i>Meconopsis cambrica</i>	-0.828	2.315	-0.320	802	923	
<i>Lunaria rediviva</i>	16.91	49.05	0.587	-0.550	0.589	-0.204	865	200	<i>Asarum europaeum</i>	-0.794	0.664	-0.308	1150	200	
<i>Epimedium alpinum</i>	16.41	44.59	0.153	-0.564	2.271	-0.201	318	0	<i>Mateuccia struthiopteris</i>	-0.390	0.144	-0.287	898	0	
<i>Asarum europaeum</i>	19.39	50.16	0.732	-0.549	0.460	-0.197	700	0	<i>Corydalis intermedia</i>	-0.752	-0.688	-0.284	1173	170	
<i>Meconopsis cambrica</i>	-2.24	47.76	0.219	-0.643	2.070	-0.189	323	467	<i>Stellaria holostea</i>	-0.591	0.355	-0.274	974	0	
<i>Mateuccia struthiopteris</i>	-20.47	57.64	0.714	-0.257	0.159	-0.143	726	0	<i>Lunaria rediviva</i>	-0.766	0.866	-0.258	1145	193	
<i>Cardamine bulbifera</i>	17.69	50.14	0.722	-0.429	0.411	-0.132	613	0	<i>Epimedium alpinum</i>	-0.776	3.358	-0.241	954	219	
<i>Corydalis intermedia</i>	16.13	53.85	0.537	-0.526	0.748	-0.124	854	0	<i>Corydalis cava</i>	-0.689	0.715	-0.172	985	60	
<i>Ranunculus platanifolius</i>	13.42	49.58	0.400	-0.505	1.128	-0.054	807	413	<i>Cardamine bulbifera</i>	-0.582	0.802	-0.147	1030	0	
<i>Corydalis cava</i>	16.34	48.83	0.723	-0.450	0.574	-0.035	590	0	<i>Corydalis solida</i>	-0.557	0.668	-0.106	920	60	
<i>Cardamine heptaphylla</i>	5.33	45.69	0.249	-0.555	2.162	-0.016	387	380	<i>Hymenophyllum tunbrigense</i>	-0.553	1.255	-0.088	681	320	
<i>Moehringia muscosa</i>	14.69	45.37	0.276	-0.451	1.648	0.003	586	614	<i>Ranunculus lanuginosus</i>	-0.580	1.248	-0.082	1118	333	
<i>Corydalis solida</i>	16.53	48.78	0.675	-0.367	0.551	0.005	580	0	<i>Cardamine heptaphylla</i>	-0.694	2.738	-0.011	843	614	
<i>Helleborus niger</i>	13.16	46.62	0.137	-0.328	2.725	0.044	533	683	<i>Moehringia muscosa</i>	-0.600	2.229	-0.015	999	928	
<i>Hymenophyllum tunbrigense</i>	-5.98	52.47	0.370	-0.321	1.047	0.066	333	187	<i>Helleborus niger</i>	-0.497	4.292	0.091	1109	1230	
<i>Phyllitis scolopendrium</i>	7.79	47.51	0.671	-0.331	0.614	0.091	450	108	<i>Ranunculus lanuginosus</i>	-0.460	1.044	0.109	656	140	
<i>Ranunculus lanuginosus</i>	16.54	48.98	0.546	-0.328	0.836	0.128	545	0	<i>Phyllitis scolopendrium</i>	-0.436	0.857	0.139	746	265	
<i>Polystichum setiferum</i>	5.61	46.39	0.560	-0.318	1.060	0.275	442	0	<i>Polystichum setiferum</i>	-0.429	1.419	0.366	998	320	
<i>Helleborus foetidus</i>	3.01	45.95	0.509	-0.367	1.344	0.316	392	0	<i>Eranthis hyemalis</i>	-0.834	9.724	0.377	796	676	
<i>Eranthis hyemalis</i>	13.21	44.2	0.124	-0.626	7.766	0.341	441	430	<i>Helleborus foetidus</i>	-0.492	1.766	0.417	704	240	
<i>Woodwardia radicans</i>	4.33	41.64	0.093	-0.045	11.145	1.026	654	486	<i>Woodwardia radicans</i>	-0.937	1.684	0.747	851	680	
<i>Paonia mascula</i>	11.93	43.08	0.154	-0.123	8.868	1.245	530	309	<i>Paonia mascula</i>	-0.276	10.879	1.402	801	545	
<i>Culicita macrocarpa</i>	-6.97	40.25	0.037	1.289	19.385	2.000	500	389	<i>Culicita macrocarpa</i>	1.246	10.720	1.639	646	290	

Southern refugial area

During past glacials the European temperate forest flora survived in small refuges scattered across southern Europe (e.g. Willis 1996, Willis et al. 2000), and it is thought that intermediate warm stages as well as glacial persistence in the southern refuges is crucial for the long-term survival of temperate forest taxa in Europe (Bennett et al. 1991, Willis 1996). For this reason, we also modelled the net change in suitability for each species within the southern refugial area, here defined as Europe south of a line that runs along the south slopes of the Alps (based on Willis 1996, Willis et al. 2000). Computations for this region exclude *Actaea erythrocarpa*, which occurs from Scandinavia into Siberia, but is absent from southern Europe.

Land-use patterns and potential migration routes

A species' ability to migrate in response to climate change depends on its dispersal potential and on the availability of suitable habitat along the potential migration routes. Colonisation success is strongly related to the amount of suitable habitat. Honnay et al. (2002) showed empirically that the colonisation success of temperate forest herbs strongly depended on the degree of forest cover in two Belgian landscapes (Honnay et al. 2002). Furthermore, the simulated rates of migration for a wind-dispersed forest tree dropped sharply when habitat availability was < 25% (Collingham and Huntley 2000). Hence, we used present-day forest cover as a proxy for habitat availability, assuming that temporal and land-use constraints will prevent major changes in the geographical distribution of forested land over the next 100 yr.

Data on current forest cover stem from the 'Global 500 m Tree Cover Product' from Terra MODIS (<<http://glcfapp.umiacs.umd.edu/data/>>). The map shows proportional estimates of tree cover using a 500 m resolution. The grid was resampled to the resolution of the other data sets. A measure of migration resistance was developed based on % tree cover:

The inverse tree cover grid was used as an approximation for migration resistance (the lower the forest cover, the higher the resistance to forest herb dispersal). Resistance is assumed to approach zero when forest cover is close to 100%. Based on Collingham and Huntley (2000) resistance was set to ca 80% of maximum with a forest cover of 25% and increasing exponentially to maximum when forest cover approaches zero. Optimal dispersal routes were determined using Cost Weighted Distance mapping and the Shortest Path function (Anon. 2002). These functions are used to find the shortest (or least-cost) path from a set of sources to a set of destinations, e.g. sites with future suitable climatic conditions. The number of potential dispersal

routes is virtually unlimited depending on where start- and ending points are placed. To demonstrate some of the most important routes, we have used a number of suggested European plant diversity hotspots (see Fig. 1 in Bakkenes et al. 2002) and some important forest areas as starting points. In light of our results on the potential range changes needed to track suitable climatic conditions under the near-future global warming, we placed the migration end points in northeastern Scandinavia. The resulting list of potential migration paths is not exhaustive and should be seen as a collection of important routes.

Results

Species and their response to the climatic change scenario

We note a general good agreement of the estimated suitability under the present climate and the observed current distribution (Fig. 2). However, the variable r/p ratio (mean = $39.7 \pm 24.8\%$ SD, range = 4.4–85.3% – see Table 2) suggests that the species vary a lot in the degree to which they occupy the presently climatically suitable areas in Europe. The low mean r/p suggest that many of our study species are absent from large areas of suitable climate and thus could be said to have poor range-filling capacity. We note that the naturalised ranges (not used in the model building) were generally well predicted by the model (Fig. 2).

As can be seen from Fig. 2 that the predicted consequences of the climate change scenarios vary a lot between species: *Cimicifuga europaea* is an example of a eastern species with little or no overlap between its current distribution and the future potential distribution under the two scenarios. The wide-ranging, but northern *Equisetum sylvaticum* is predicted to loose large proportions of its southern distribution, but continuing to experience climatically suitable conditions under both scenarios in much of its northern range. *Asarum europaeum* is an example of a widespread nemoral species, which may loose much of its climatically suitable range in southern and central Europe, but potentially expand to the north and northeast. *Eranthis hyemalis* is an example of a southern-eastern nemoral species, whose currently restricted range in southern Europe leaves large climatically suitable parts of central Europe empty. Under future climate change it could expand greatly northwards given sufficient migration. *Helleborus foetidus* and *Paeonia mascula* exemplify south-western removal and mediterranean/submediterranean species, respectively, whose climatically suitable area may likewise expand dramatically northwards.

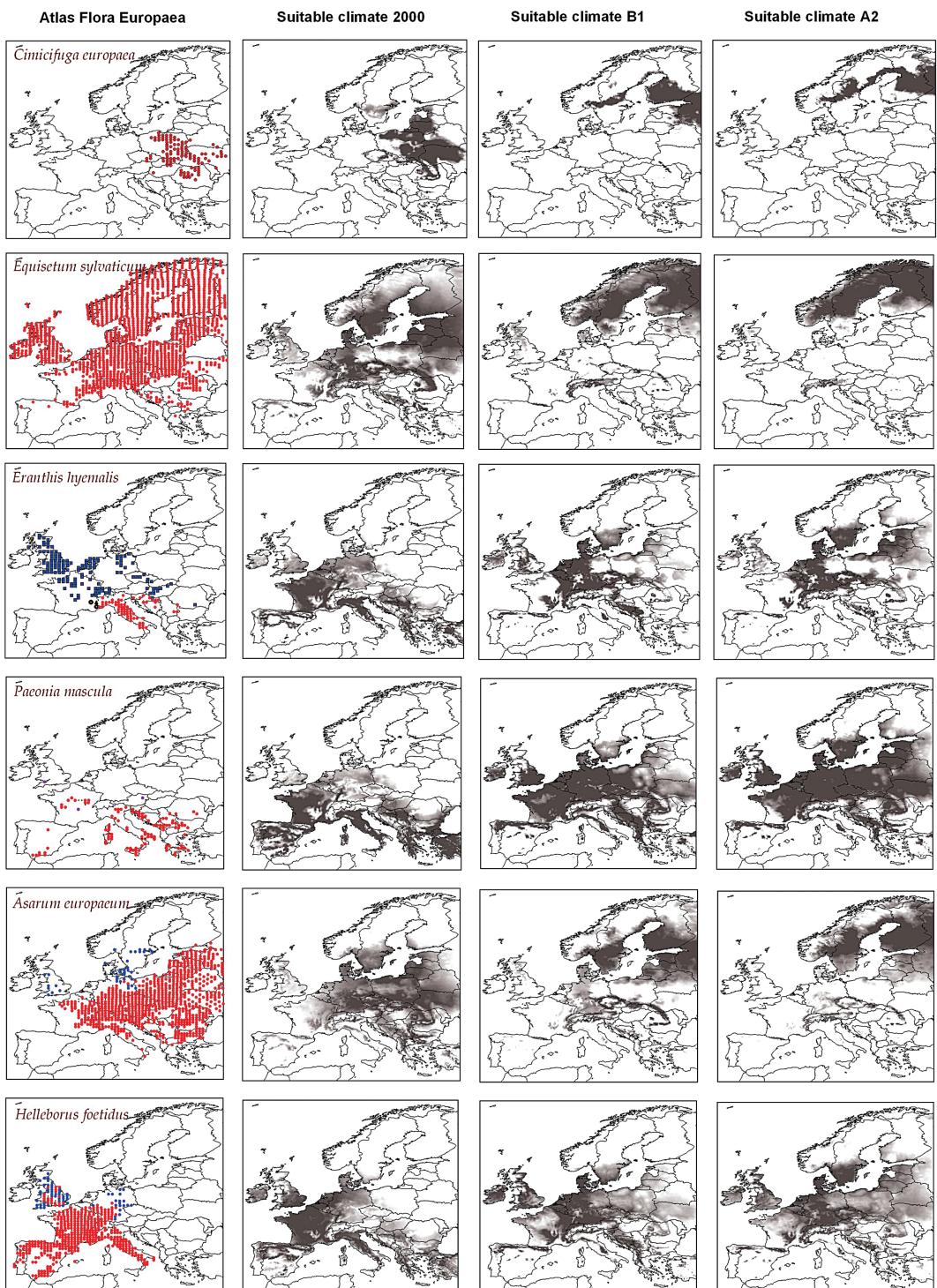


Fig. 2. Examples of distribution maps. The first column of maps shows recorded distribution based on *Atlas Flora Europaea*. Column 2 shows modelled suitable climate today. Column 3 shows suitable climate under scenario B1 and the last column shows suitable climate under scenario A2. Suitable climate is indicated by a gray scale from white (not suitable) to dark gray (very suitable). Note, that this choice of color makes it difficult to separate 0-values (i.e. pixels totally outside the environmental envelope) from pixels with low climatic suitability (e.g. *Equisetum sylvaticum* in northern Scandinavia). The species are: *Cimicifuga europaea*, *Equisetum sylvaticum*, *Asarum europaeum*, *Eranthis hyemalis*, *Helleborus foetidus*, and *Paeonia mascula*. Red dots show recorded natural distribution; blue dots show records of naturalised occurrences.

General trends

Moderate losses in the total suitable area in Europe are predicted for most species under both scenarios (Table 1A). However, the predicted changes are very variable, with one species (*Actaea erythrocarpa*) experiencing total loss of suitable areas in Europe under the A2 scenario, while the total suitable area is predicted to show large increases for some other species. Large losses in suitability within the recorded distribution were seen for most (but not all) species under both scenarios (Table 1B, Fig. 3), with losses predicted to be even more severe in the southern refugial region than in Europe as a whole (Table 1C).

A general change in location (range centroid) of the total suitable area was predicted: The total suitable area will on average move strongly northwards and moderately eastwards under B1 and more strongly so under A2. (Fig. 4A). For two species with a current southern distribution (*Woodwardia radicans* and *Culcita macrocarpa*), however, the displacements is towards northwest rather than northeast, reflecting the loss of suitable climate in the eastern part of the Mediterranean basin caused especially by an expected decrease in precipitation.

The average measured range-shift needed (based on difference between the predicted cross-European range centroid under a given scenario and the current range centroid for occupied AFE cells; see Table 2) per year is 5.6 km under the B1 scenario (max: 9.6 km, min: 2.4 km, SD: 1.8 km) and 9.3 km under the A2 scenario (max: 13.6 km, min: 6.5 km, SD: 1.8 km). We also measured range-shift based on difference between the predicted cross-European range centroid under a given scenario and closest occupied AFE cell (Table 2). This present-

margin-to-new-centroid migration rate, which may better reflect the actual distance a species need to migrate to fill a major part of its potential range under a given scenario, is 2.1 km under the B1 scenario (max: 8.2 km, min: 0 km, SD: 2.6 km) and 3.9 km under the A2 scenario (max: 12.3 km, min: 0 km, SD: 3.7 km).

Migration routes

Figure 4B shows possible migration routes along which dispersal of forest plant herbs is most likely taking the current forest cover into consideration. The full line shows least-cost paths when the Baltic Sea (or water in general) is considered an un-crossable barrier. The hatched line shows an alternative pattern if water is set to pose a barrier of similar strength as unforested land, i.e. allowing that species are able to cross the Baltic Sea from northern Germany to the southern tip of Sweden. This opens up a new entry to Scandinavia where a substantial number of species will find suitable climatic conditions under the A2 scenario (see Fig. 2 for some examples). Those species that are unable to cross the Baltic Sea, clearly, are forced to move eastwards instead of north thus making the length of the dispersal route considerably longer. The map also shows the importance of maintaining existing large tracts of forest or even establishing new forest to ease migration. Forest complexes surrounding the Alps and in Eastern Europe could play a major role in forest herb migration forced by global warming.

Index of Predicted Range Change

Table 2 shows that the forest herbs analysed in this study may roughly be divided in four groups in terms of the likely net range impact of global warming. The first group consists of one species – *Actaea erythrocarpa* – expected to be at high risk of extinction in Europe under global warming. The second group consists of eight species that will experience moderate to severe range losses in case of climatic change. Among these species are *Cimicifuga europaea*, *Equisetum sylvaticum* and *Stellaria holostea*. The third consists of 11 species having index values close to zero, where losses of currently occupied areas could be expected to be neutralised by expansions into new areas of suitable climate. The last group includes six species which may actually benefit from global warming (given sufficient dispersal): *Culcita macrocarpa*, *Eranthis hyemalis*, *Helleborus foetidus*, *Paeonia mascula*, *Polystichum setiferum*, and *Woodwardia radicans*. The species that are predicted to experience the greatest net range losses tend to have northern or eastern range centroids (Fig. 5).

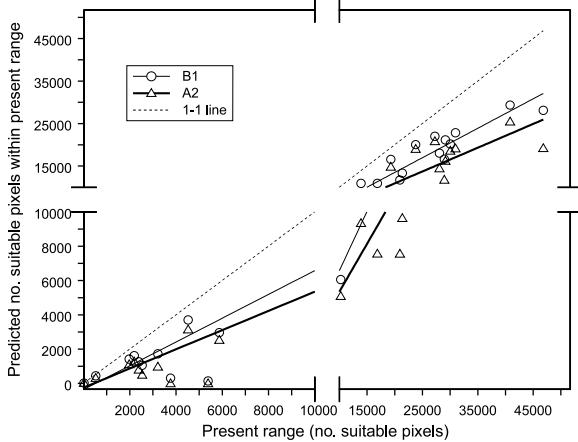


Fig. 3. Number of suitable 10' pixels within the presently occupied AFE cells across Europe for a given species under the present climate (abscissa) and the B1 and A2 scenarios (ordinate). Lines are linear least-squares regression fits. Graph axes are broken to allow high visual resolution at both small and large range sizes, simultaneously.

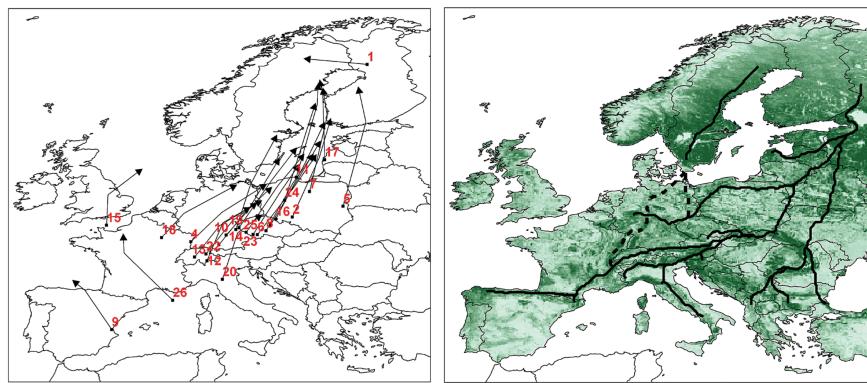


Fig. 4. Range-shift patterns for all 26 species studied (No. 1–26). Arrow bases indicate where current range centroids are and arrow heads the centroid under scenario A2. The intermediate scenario B1 is represented as a bend on most arrows. (B): potential migration routes: full lines illustrate least cost path where water cannot be crossed, while hatched lines illustrate alternative routes if water is set to base a barrier of similar strength as non-forested land. The degree of forest cover is indicated by green. Numbers refer to: 1, *Actaea erythrocarpa*; 2, *Asarum europaeum*; 3, *Cardamine bulbifera*; 4, *Cardamine heptaphylla*; 5, *Cimicifuga europaea*; 6, *Corydalis cava*; 7, *Corydalis intermedia*; 8, *Corydalis solida*; 9, *Culcita macrocarpa*; 10, *Epimedium alpinum*; 11, *Equisetum sylvaticum*; 12, *Eranthis hyemalis*; 13, *Helleborus foetidus*; 14, *Helleborus niger*; 15, *Hymenophyllum tunbrigense*; 16, *Lunaria rediviva*; 17, *Matteuccia struthiopteris*; 18, *Meconopsis cambrica*; 19, *Moehringia muscosa*; 20, *Paeonia mascula*; 21, *Phyllitis scolopendrium*; 22, *Polystichum setiferum*; 23, *Ranunculus lanuginosus*; 24, *Ranunculus platanifolius*; 25, *Stellaria holostea*; 26, *Woodwardia radicans*. Note that *Actaea erythrocarpa* (1) has no suitable area left under scenario A2.

Discussion and conclusions

The modelling approach

While fuzzy climatic envelope modelling may seem simplistic compared to other approaches (see discussion

in Guisan and Zimmermann (2000)), we believe it offers several important advantages: 1) Firstly, as employed here it relates plant distributions to a set of ecological niche factors of well-established importance for plant performance and large-scale plant distributions, i.e. growing-degree days, minimum temperature, and the water balance (e.g. Sakai and Weiser 1973, Sykes et al. 1996, Stephenson 1998, Thompson et al. 1999). 2) Secondly, the model structure (whether in the rectilinear or the fuzzy version) is simple and transparent in contrast to other approaches such as Neural Networks (Berry et al. 2002, Pearson et al. 2002). Given these advantages it is no surprise that fairly simple climatic envelope models or modifications thereof remain much used in studies investigating the potential biodiversity impacts of future climate change (e.g. Shao and Halpin 1995, Sykes et al. 1996, Iverson and Prasad 1998, Box et al. 1999, Crumpacker et al. 2001, Bakkenes et al. 2002).

The fit between predicted suitability under the present climate and the observed current distributions generally appeared good (Fig. 2). However, as the low average r/p value shows, the predicted suitable areas across Europe were often twice the size or more of the observed distribution (as represented by the number of suitable pixels within the current distribution). The low r/p ratios could reflect that their present range to a large extent is limited by non-climatic factors, notably dispersal or edaphic factors, or reflect that our model have overestimated the climatic envelope of the species. We believe the low r/p values to a large extent reflect that many species have not been able to occupy their complete suitable area due to dispersal limitation (e.g. Davis 1986, also cf. Charles-Dominique et al. 2003). This argument is

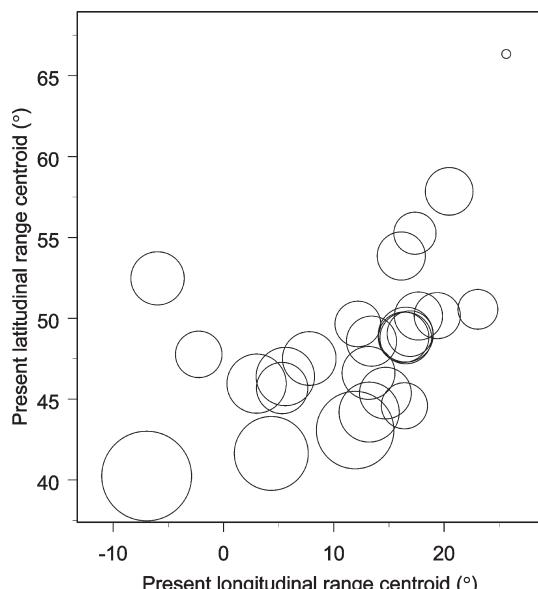


Fig. 5. The Index of Predicted Range Change (IoRPC) calculated for each species under the B1 scenario presented as a function of its present longitudinal and latitudinal range centroid. Bubble size reflects the IoRPC value, ranging from −0.962 for *Actaea erythrocarpato* to 2.0 for *Culcita macrocarpa*. The A2 scenario produced a very similar plot. See also Table 2.

supported by the observation that in most cases where our model predicted larger areas of high suitability (mostly northwards) under the current climate outside the current range, the species concerned are often more or less widespread in these areas as naturalised (see Fig. 2 for some examples, cf. Anon. 1964–1993, Hansen 1984, Stace 1997).

The valid use of static models such as bioclimatic envelopes for forecasting changes in species distribution under climatic change has been questioned (e.g. Woodward and Beerling 1997, Davis et al. 1998, review in Pearson and Dawson 2003). The current AFE distributions of many species may also include cells with only remnant or, albeit less likely given the large size of the AFE cells, sink populations (Eriksson 1996), which would bias the predicted potential range expansions upwards. Maps produced by climatic envelopes, however, should be perceived as suitability maps and not as maps predicting realised distributions (Pearson and Dawson 2003). Hence, differences in current and future suitable areas show the strength of climatic drivers and indicate where changes in species' distributions may take place. The available area of suitable climate is perhaps best regarded as representing the maximum potential distribution, which is unlikely to be fully realised due to the operation of non-climatic limiting factors such as migration limitations (e.g. Pearson and Dawson 2003). The issue of range filling is particular pertinent to forest herbs due to their notoriously slow and restricted dispersal in the modern fragmented temperate forest landscapes of North America and Europe (see below). We addressed this issue in our modelling by looking at the predicted changes not only across Europe, but also within just the presently occupied cells for a given species. The latter will be of crucial importance if migration is limited. While we therefore believe our modelling approach is likely to produce robust qualitative results, we acknowledge that it still includes many uncertainties and assumptions, the most important probably being the large uncertainties regarding the near-future climatic changes (Anon. 2001, Hulme et al. 2002). However, we attempted to address this issue by including two different climate change scenarios, an 'optimistic' as well as a 'pessimistic' scenario. An additional important uncertainty is that the direct physiological effects of increased atmospheric CO₂ concentrations were not possible to consider in our modelling with the present state of knowledge. However, the effects on plant distributions could well be large (Harrison and Prentice 2003).

Impact of global warming on plant distributions

The modelling presented here suggests that the climatic changes likely to occur over the next century could have

drastic consequences for the European forest herb flora. Even under the mild scenario, the following consequences are predicted: 1) Moderate to large losses of climatically suitable areas for most species (e.g. a 17–61% reduction in total climatic suitability for 75% of the 26 species). 2) Large losses of climatic suitability within the presently occupied range across Europe and even more drastic losses within the southern refugial region. 3) The range centroids for the total climatically suitable area will move strongly towards the northeast for most species (Fig. 4A). The required present-margin-to-new-centroid migration rates to track the potential range centroids are on average 2.1 km yr⁻¹ for the B1 scenario and 3.9 km yr⁻¹ for the A2 scenario. 4) If species are able to fill the predicted potential ranges to the same extent as they fill their present-day range, 12 out of 26 species should be able to maintain or expand their total range in Europe under B1 (i.e. those species with IoPRC > 0). Here, we will discuss the implications of these findings.

Overall, our results suggest that even under the optimistic scenario many forest herbs will either have to produce large and fast range shifts or become much reduced in European population size. The necessary migration rates are similar to those estimated by other studies of plant range shifts under near-future global climate change (Davis and Shaw 2001). While such fast migration rates are unlikely even for wind-dispersed trees (Clark et al. 1998, Davis and Shaw 2001), this problem is particularly severe for forest herbs, the majority of which are poor dispersers (e.g. Cain et al. 1998, Huntley et al. 1995) and currently exhibit slow migration rates in contiguous forest landscapes (mostly ≤ 1.5 m yr⁻¹: Matlack 1994, Brunet and von Oheimb 1998, Bossuyt et al. 1999, Bellemare et al. 2002). Furthermore, the slow migration problem is exacerbated by the modern fragmented status of the European forests (Fig. 4B), as numerous studies document a strongly negative impact of geographical isolation on forest herb colonisation of forest fragments (e.g. Peterken and Game 1984, Matlack 1994, Pitelka et al. 1997, Wulf 1997, Grashof-Bokdam and Geertsema 1998, Honnay et al. 2002). In fact, the high degree of forest fragmentation in much of Europe may severely depress migration rates of even wind-dispersed trees (Collingham and Huntley 2000). While implied migration rates during postglacial recolonisation are much higher than most currently observed forest herb dispersal rates (Cain et al. 1998), as is the case for trees as well (e.g. Clark et al. 1998, Davis and Shaw 2001), the as-yet uncertain mechanisms may not be functional in the modern landscape (e.g. Poschlod and Bonn 1998). Notably, free-ranging large herbivores may be crucial for the achievement of efficient long-distance dispersal in forest herbs and many other plants (Pakeman 2001), but herbivores with sufficiently large territory sizes are rare or absent in much Europe today.

(also cf. Pitelka et al. 1997). Thus, natural dispersal of most forest herbs is unlikely to allow tracking of the changing climate (Honnay et al. 2002). However, for species used in horticulture human-mediated dispersal may provide a high rate of long-distance dispersal (Hodkinson and Thompson 1997, Pitelka et al. 1997), as suggested by the large naturalised range of many such species (e.g. Hansen 1984, Stace 1997). These considerations indicate that the predictions regarding suitability changes within the currently occupied range of the study species (i.e. assuming no dispersal) are more realistic than those based on changes in total suitability across Europe (i.e. assuming no dispersal limitation), except in the case of unintentional or intentional (as suggested by Honnay et al. 2002) human-mediated dispersal. Some species studied here are used as ornamentals outside their natural range (e.g. *Eranthis hyemalis*, *Helleborus foetidus* and *Asarum europaeum*) and are known to naturalise far beyond their current native ranges (see Fig. 2). If naturalisation occurs within the expected future climatic range this may greatly benefit their chances of coping with climatic change.

The disproportionately strong suitability losses predicted for the southern refugial region are of particular concern, since this region is also of special importance for the European forest flora. First of all, long-term ($\geq 100\,000$ yr) survival of European mesic temperate plants, not only the southern, but also most of the widespread species, seems to depend on survival in the southern refugia not only during glacial periods, but also during warm stages (Bennett et al. 1991, Willis 1996, also cf. Vogel et al. 1999). The importance of parts of southern Europe as refuges reflect that climate changes here have been small relative to the available topographic relief (Vogel et al. 1999), allowing plants to track suitable climatic conditions by migrating across small geographic distances. Secondly, reflecting its refugial importance southern Europe also harbours the majority of restricted-range species as well as most of the genetic diversity within the more widespread species (Vogel et al. 1999, Petit et al. 2003, also cf. Bakkenes et al. 2002). Thus, loss of southern populations could cause a disproportionate loss of phytodiversity at both within-species and species levels in the near as well as the more distant future (such as when a future glacial period sets in, cf. e.g. Berger and Loutre (2002)). Even when disregarding the longer-term threat posed by the loss of southern populations, the possible climatic changes over the next hundred years may cause the extinction of some species throughout their European range. As our modelling shows boreal forest species will be particularly threatened (as exemplified by *Actaea erythrocarpa*). Analogously, three boreal or boreonemoral conifer species became regionally (in one case also globally) extinct in southeastern North America during the rapid global warming of the glacial-postglacial transition

(Davis and Shaw 2001). Conversely, we may expect warm-temperate and subtropical forest herbs to expand into much of central Europe, while increased drought is likely to reduce their realised and potential distributions in southern Europe (Fig. 2). Given the slow current natural migration rates of forest herbs, it is to be expected that much of this expansion will be human-mediated, notably through horticulture, and may well include species not native to Europe. The expansion of thermophilic woody species, exotic as well as European species, is already being observed in southern parts of central Europe and montane areas of southern Europe (Walther 2000, Peñuelas and Boada 2003). While such expansions may be positive from the point of view of conserving southern native species, they may hasten the demise of remnant populations (sensu Eriksson 2000) of nemoral species and thus at the same time pose a conservation problem.

Implications for conservation planning

The present study deals with the consequences of climate change on a relatively small sample of forest herbs, but the results, nevertheless, raise important questions concerning biodiversity management in the light of climate change. Design of reserves in general presupposes a constant climate and fixed species distribution ranges; the degree of change caused by both climate scenarios studied here shows that both assumptions may well be false. Hannah et al. (2002a,b) suggest improving traditional conservation planning by involving collaboration between biogeographers, ecologists, modellers and conservationists. This type of collaboration should ideally result in "Climate Change-integrated Conservation Strategies" (CCS) designed to respond adequately to changing biogeographic patterns induced by global warming (Hannah et al. 2002a, Midgley et al. 2003). The first step of a CCS is an assessment of potential climate change impacts on biodiversity (regional modelling). The results of this assessment may then be used to expand or adjust the network of protected areas and to manage land-use outside protected areas (the 'matrix') to facilitate dispersal or even maintain populations in transition.

Midgley et al. (2003) note that species react individually to climate change which means that conservation strategies based on biomes or habitats are inadequate. We cannot expect, however, to find the necessary funding to formulate individual management plans for all species and need instruments to prioritise species in critical danger. The Index of Predicted Range Change described in this paper weights future distribution loss caused by climate change against potential gain and gives a rough indication of which species probably will require most immediate attention under a changing

climate. The index is easy to calculate based on atlas data and represents a crude first prioritisation of species in need of conservation management.

In the light of CCS, this study can be seen as an initial assessment of how climate change may change the distribution patterns of European forest herbs. The findings of the assessment provide the following preliminary suggestions for mitigation of climate change impact on European forest herb biodiversity: 1) Lessen forest fragmentation throughout Europe, protect northern and eastern outlier populations of forest herbs, and maintain healthy populations of long-distance dispersal agents to increase natural migration rates. An option is to create new forest on marginal agricultural land, but this should be considered only on areas without conservation value for semi-natural open habitats. 2) Human-mediated translocation of forest herb populations will most likely also be necessary to allow tracking of suitable climate (Honnay et al. 2002) as well as to avoid excessive losses of genetic diversity through extirpation of the southern, more diverse populations. 3) Closely monitor the status of boreal and subalpine forest species in particular, as these species are likely to be most threatened by global warming. South-European populations of all forest species should also be a focus for monitoring due to their crucial long-term importance in conjunction with the likelihood that they will come under particular press from global warming. 4) Increased protection and restoration of forest habitats in southern montane areas (due to their crucial long-term importance) to enhance the possibilities for in situ survival and short-distance climate tracking of the southern forest herb populations.

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