

Quantifying components of risk for European woody species under climate change

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Abstract

Estimates of species extinction risk under climate change are generally based on differences in present and future climatically suitable areas. However, the locations of potentially suitable future environments (affecting establishment success), and the degree of climatic suitability in already occupied and new locations (affecting population viability) may be equally important determinants of risk. A species considered to be at low risk because its future distribution is predicted to be large, may actually be at high risk if these areas are out of reach, given the species' dispersal and migration rates or if all future suitable locations are only marginally suitable and the species is unlikely to build viable populations in competition with other species. Using bioclimatic models of 17 representative European woody species, we expand on current ways of risk assessment and suggest additional measures based on (a) the distance between presently occupied areas and areas predicted to be climatically suitable in the future and (b) the degree of change in climatic suitability in presently occupied and unoccupied locations. Species of boreal and temperate deciduous forests are predicted to face higher risk from loss of climatically suitable area than species from warmer and drier parts of Europe by 2095 using both the moderate B1 and the severe A1FI emission scenario. However, the average distance from currently occupied locations to areas predicted suitable in the future is generally shorter for boreal species than for southern species. Areas currently occupied will become more suitable for boreal and temperate species than for Mediterranean species whereas new suitable areas outside a species' current range are expected to show greater increases in suitability for Mediterranean species than for boreal and temperate species. Such additional risk measures can be easily derived and should give a more comprehensive picture of the risk species are likely to face under climate change.

Keywords: dispersal, distance, distribution, distribution modelling, extinction risk, forests, migration, range shifts

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Introduction

Biotic responses to anthropogenic climate change are already apparent (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003) and are likely to continue in future (Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a). The degree to which a species has been and will be affected by climate change depends in

part on the size of its current and future range, its environmental tolerance, and its dispersal capacity.

Conventional attempts to assess extinction risk have typically made two important, simplifying assumptions. The first key assumption concerns the expected level of colonization of new areas that become climatically suitable for a species. Given the lack of specific dispersal and habitat information for most taxa, most researchers have estimated the consequences of climate change under two extreme alternatives; that species can disperse freely and achieve their new distributions, or that species are unable to move at all (e.g. Bakkenes

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et al., 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a, b). These are useful boundaries, but neither extreme is particularly likely: it is likely that some sort of intermediate level of colonization will be achieved by most taxa. Where a particular organism falls between the extremes of zero and complete dispersal will depend on the (interactions of) habitat specificity of the taxon (Warren *et al.*, 2001), the landscape structure (Hill *et al.*, 2001; Thomas *et al.*, 2001), the distance to be moved and, given the importance of long-distance dispersal events, the time frame considered (Clark, 1998; Higgins & Richardson, 1999; Guisan & Thuiller, 2005). Few attempts have been made to incorporate intermediate dispersal scenarios in distribution models (e.g. Peterson *et al.*, 2001; Iverson *et al.*, 2004) and those that have often assume identical dispersal abilities for a wide range of species and landscapes. Until such time as species and landscape-specific dispersal scenarios are better understood, we need to seek simplifications that rely neither on the assumption of complete nor zero dispersal. A species is more likely to colonize climatically suitable regions that are close to its existing distribution than to colonize habitats that are far away: the complete vs. zero dispersal approach to extinction risk assessment would make no distinction between these likelihoods in the instance that current and projected distributions are disjunct. Thus, existing analyses fail to utilize a substantial portion of the information available in the projected distributions.

The second simplifying assumption is that species will die out within regions that are predicted to become climatically unsuitable for them (Peterson *et al.*, 2001; Midgley *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005a). Authors of these studies have been careful to specify that the time scales of these extinctions are uncertain, and many different factors may lead to variation in rates of decline. For instance, adding a periodic disturbance to a forest dynamics simulation model including *Picea abies* can shorten the time to extinction following a warming event by >300 years (M. T. Sykes, unpublished data). Using threshold models that predict alternatively the presence or absence of an organism, species are deemed 'extinct' in areas that fall below their thresholds for persistence. However, in assessing extinction risk, no distinction is made between areas that are just below the threshold for persistence, and those where the predicted probability of occurrence is very low or zero. Clearly, one would expect a species to be more likely to die out from an area, and to do so most rapidly, in the regions of lowest suitability, and most likely to persist in regions of high probability of occurrence in both periods. By truncating the output of distribution models to presence/absence data, useful information is being ignored.

We present two additional measures of risk in order to complement previous risk assessments based on area loss alone: (a) the distance to the nearest and to all projected climatically suitable areas and (b) the degree to which currently occupied and unoccupied locations are predicted to change in climatic suitability. Changes in area, distance and suitability are quantified and compared here for 17 European tree and shrub species using pre- (1945) and postwarming (1995, 2045, 2095) projected climate suitability maps. Different aspects of risk are in some cases negatively correlated with one another, and thus add important and necessary information when assessing climate change risk.

Methods

Climate data

Four climate variables relevant for the ecophysiology of European woody species (Woodward, 1987) were derived from a 10' × 10' resolution gridded European window approximately covering 11°W, 34°N, 32°E, 72°N (Mitchell *et al.*, 2004): mean temperature of the coldest month (*Tcold*), mean temperature of the warmest month (*Twarm*), growing degree days sum >5°C (GDD5) and a drought index $Drought = 1 - (\text{actual transpiration} / \text{equilibrium evapotranspiration})$ with soil water capacity set to 150 mm. These variables have been shown to be good predictors of the distributions of the selected species and further details are given in Sykes & Prentice (1996), Sykes *et al.* (1996) and Walther *et al.* (2005).

The climate variables were calculated for two observed and two projected time periods: 1945 (1931–1960 average, hereafter referred to as the prewarming or 1945 period), 1995 (1991–2000 average), 2045 (2041–2050 average) and 2095 (2091–2100 average) using CRU observed climate data and projections from the HadCM3 GCM (Mitchell *et al.*, 2004). Two emission scenarios were used in order to assess the minimum and maximum expected change in climatic conditions: B1, with the smallest projected average temperature increase of all scenarios of 2°C by 2100, and A1FI, with the largest projected average temperature increase of all scenarios of 4.8°C by 2100 (IPCC, 2001).

Climate suitability maps of tree and shrub species

A nonexhaustive set of 17 European tree and shrub species for which both ecophysiological responses to the climate variables and present-day European distributions are well known was selected (Table 1). The selected species are representative of all major European terrestrial biomes (Haxeltine & Prentice, 1996;

Sitch *et al.*, 2003). European distributions for all but one species were obtained from Atlas Florae Europaeae (Jalas & Suominen, 1972, 1973, 1976, 1979, 1980, 1983, 1986, 1989, 1991, 1994) and that of *Ilex aquifolium* was taken from Hulten & Fries (1986). These distributions are surrogate distribution maps comprising records from mainly the second but also the first half of the 20th century. For the purpose of this study, we assumed that these species distributions (a) reflect the most accurate approximation of present-day species distributions at European scale and (b) are the result of the species' responses to the climatic conditions of the last normal climate period 1931–1960. All species distributions were standardized to a $0.5^\circ \times 0.5^\circ$ UTM grid on the same European window as the climate data.

We resampled the $10' \times 10'$ climate data with the $0.5^\circ \times 0.5^\circ$ UTM grid and used the latter resolution to fit generalized additive models (GAMs) of the present-day species presences/absences and the 1945 climate variables with binomial errors, a logit link function and smoothing splines in S-Plus (Venables & Ripley, 2002). The models were used to predict climatic suitability (i.e. probability of occurrence) of each species at the $10' \times 10'$ resolution for all four time periods. Although GAMs provide a flexible and robust framework for species distribution modelling, the projected distributions are likely to differ when different modelling methods are used (Thuiller *et al.*, 2004; Araújo *et al.*, 2005). We, therefore, repeated all analyses using two alternative methods: Generalised Linear Models (GLMs) with binomial errors, logit link and including linear and second-order polynomial terms, and classification trees (CTs) with a minimum node deviance of 0.01 and the default shrinking rules given in S-Plus (Venables & Ripley, 2002). Overfitting of the CT models was avoided by checking the node number/deviance reduction plots (Bell, 1999).

Model evaluation

Downscaling the data to a different resolution allowed for an independent evaluation of the models using the two measures: Cohen's κ , and AUC values of the ROC statistic (Araújo *et al.*, 2005). κ was calculated for different probability cut-offs (step size 0.1) at the $10'$ resolution. If at least one $10'$ cell within a 0.5° cell had a higher probability than the cut-off value, the 0.5° cell was considered as being occupied by that species. κ was then calculated from the predicted presence/absence matrix using the climate from the 1945 period and the observed presence/absence matrix at 0.5° resolution. The probability value which maximized κ was used as a cut-off to assign species presences/absences to each $10'$ cell for further analyses. κ values range between 0 and 1

and values between 0.4 and 0.75 may be considered as showing good agreement between observed and predicted species occurrences, while values <0.4 indicate poor and values >0.75 indicate excellent agreement (Landis & Koch, 1977). Area under the curve (AUC) values were calculated by assigning to each 0.5° cell the highest probability value of any $10'$ cell within it and calculating the ROC curve of sensitivity vs. (1-specificity) at 0.5° resolution using the roc() function in S-Plus. AUC values range between 0.5 and 1, for which Swets (1988) suggests the following interpretation: $AUC > 0.9$: excellent agreement between observed and predicted distribution; $0.8 < AUC < 0.9$: good; $0.7 < AUC < 0.8$: fair; $0.6 < AUC < 0.7$: poor; $0.5 < AUC < 0.6$: fail. For the majority of modelling methods and species, the predicted and observed 1945 distributions were in good agreement (Table 1). The predictions were only poor when using GLMs for *Abies alba* and *Larix decidua*.

Measures of risk

All measures of risk were calculated using the modelled species distributions on the $10' \times 10'$ European grid. Based on changes in climatically suitable areas, changes in distance to these areas and changes in climatic suitability between 1945 and future periods, we quantified risk for each species using the following six measures:

- (I) *Change in climatically suitable area (cut-off, full dispersal)*: We calculated the area of each climatically suitable cell (see Ohlemüller *et al.*, 2006), summed up the total area of all cells predicted to be climatically suitable in the four time periods and calculated the percent change between the 1945 and the three later periods. Climatically suitable areas were identified using the cut-off which maximized κ for the 1945 period, as described above. High percentage area loss indicates high risk, high percentage area gain indicates no risk.
- (II) *Change in climatically suitable area (cut-off, no dispersal)*: As in (I) but assuming that a species can only occur in a cell in the later periods when it was already predicted to be present in that cell in the 1945 period. High percentage area loss indicates high risk, low percentage area loss indicates low risk.
- (III) *Change in distance to nearest climatically suitable cell (cut-off, full dispersal)*: For each cell (focal cell) which was modelled as suitable in the 1945 period, the distance to the nearest cell (excluding the focal cell) with suitable conditions in the 1945 period and the three later periods was calculated (see Ohlemüller *et al.*, 2006). The difference in average

Table 1 Seventeen European tree and shrub species, their prevalence (% cells occupied in Europe) and the accuracy of predictions of their 1945 distributions using three different modelling methods (generalized additive models – GAMs; generalized linear models – GLMs; classification trees – CTs) and two measures of model accuracy (κ , AUC – see text for details)

Species	Prevalence (%)	GAM		GLM		CT		Biome affinity
		κ	AUC	κ	AUC	κ	AUC	
1. <i>Abies alba</i>	17	0.55	0.85	0.47	0.67	0.72	0.96	T/Bmix, Tc
2. <i>Betula nana</i>	24	0.79	0.97	0.75	0.97	0.86	0.99	Bd, T/Bmix, Bc
3. <i>Betula pendula</i>	69	0.74	0.94	0.72	0.91	0.81	0.97	Td, T/Bmix, Bc
4. <i>Betula pubescens</i>	64	0.73	0.93	0.70	0.92	0.80	0.96	Td, T/Bmix, Bc
5. <i>Castanea sativa</i>	26	0.58	0.88	0.51	0.84	0.73	0.95	T/Bmix, Te
6. <i>Fagus sylvatica</i>	43	0.67	0.91	0.65	0.81	0.80	0.96	Td, T/Bmix
7. <i>Ilex aquifolium</i>	39	0.71	0.95	0.70	0.92	0.81	0.97	Td, T/Bmix
8. <i>Juniperus communis</i>	72	0.58	0.87	0.55	0.85	0.74	0.95	Td, T/Bmix, Bc
9. <i>Juniperus oxycedrus</i>	12	0.58	0.90	0.48	0.88	0.72	0.97	Xe, T/Bmix, Tc
10. <i>Larix decidua</i>	6	0.44	0.90	0.36	0.71	0.70	0.98	T/Bmix
11. <i>Picea abies</i>	41	0.76	0.95	0.73	0.94	0.84	0.98	Bc, Tc, T/Bmix
12. <i>Pinus halepensis</i>	7	0.53	0.94	0.49	0.93	0.74	0.99	Tc, T/Bmix
13. <i>Pinus sylvestris</i>	55	0.74	0.93	0.72	0.93	0.83	0.97	T/Bmix, Bc
14. <i>Quercus coccifera</i>	12	0.67	0.95	0.62	0.94	0.80	0.98	Xe, Te
15. <i>Quercus ilex</i>	15	0.60	0.92	0.59	0.91	0.78	0.97	Te, Td, T/Bmix
16. <i>Quercus pubescens</i>	27	0.62	0.89	0.56	0.81	0.73	0.95	Te, Td, T/Bmix
17. <i>Quercus robur</i>	60	0.73	0.92	0.70	0.89	0.81	0.96	Td, T/Bmix

Biome affinity indicates the main biomes in which the species are typically found (listed for each species in decreasing importance): Bc, boreal conifer forest/woodland; Bd, boreal deciduous forest/woodland; T/Bmix, temperate or boreal mixed forest; Tc, temperate conifer forest; Td, temperate deciduous forest; Te, temperate broadleaved evergreen forest; Xe, xeric woodland/scrub.

distance to the nearest suitable cell between 1945 and the three later periods indicates the risk for each species: increasing distance to the nearest climatically suitable cell indicates high risk, decreasing distance to the nearest climatically suitable cell indicates low risk.

- (IV) *Change in average distance to all climatically suitable cells (cut-off, full dispersal)*: As in (III) but calculating the average distance to all suitable cells. Increasing average distance to all climatically suitable cells indicates high risk, decreasing average distance to all climatically suitable cells indicates low risk.
- (V) *Change in average climatic suitability in already occupied cells (no cut-off)*: For all cells suitable in 1945 (as defined in I), the change in probability of occurrence between the 1945 and the later time periods was calculated and the average of all cells was taken. A negative average change indicates that conditions at locations predicted suitable in the 1945 period will be less favourable in the future (high risk) while a positive change indicates that conditions for these cells will be more favourable in the future (low risk).
- (VI) *Change in average climatic suitability in presently unoccupied cells (no cut-off)*: For all cells not suitable in 1945 (as defined in I), the change in probability

of occurrence between the 1945 and the later time periods was calculated and the average of all cells suitable in 1945 was taken. A negative average change indicates that conditions at locations predicted not suitable in the 1945 period will be even less favourable in the future (high risk) while a positive change indicates that conditions for these cells will on average be more favourable in the future (low risk).

The species were then ranked according to their level of risk (1 = lowest risk, 17 = highest risk) and plotted against their observed range size in 1945 to investigate the relationship between 1945 range area and the risk status assigned to each species using the six different risk measures. We checked for the effect of the three different modelling methods by calculating Spearman's ρ rank correlation coefficient between ranks assigned to each species by each risk measure, using the three different modelling methods. High values indicate high congruence between modelling methods. Finally, we compared the rank order between all pairs of risk measures by calculating Spearman's ρ rank correlation coefficient with high values indicating that the species were ranked in similar order by the different risk measures.

Results

Risk from changes in climatically suitable areas

Risk measures I and II quantify the risk the 17 investigated European tree species are likely to face from changes in climatically suitable areas. By 2095, the lowest-risk species identified by full dispersal area change (measure I), *Pinus halepensis*, is predicted to gain between 303% (B1 scenario) and 450% (A1FI scenario) of its area predicted suitable in 1945 (Table 2). The highest-risk species, *A. alba*, is predicted to lose more than 99% of its climatically suitable area under both emission scenarios. Eleven out of the 17 investigated species are predicted to lose climatically suitable area by 2095 under the moderate B1 scenario (Table 2, Fig. 1). Species gaining climatically suitable area are mainly

those of temperate or xeric Mediterranean environments. The three modelling methods rank the species in a similar way using when using risk measure I as indicated by highly significant positive rank correlation coefficients (Table 3). When using GAMs, risk measure I is significantly ($P < 0.01$) positively correlated with all other risk measures apart from measure IV (change in distance to all climatically suitable cells) for which there is a negative relationship, with GLMs and CTs showing a similar trend (Table 4).

Using percentage area loss with no dispersal (risk measure II), the lowest-risk species, *Quercus coccifera* is predicted to lose less than 1% (B1) or 15% (A1FI) of its 1945 area by 2095, whereas *L. decidua* and *A. alba* are considered the highest-risk species, both predicted to lose 100% of their climatically suitable area by 2095 under both scenarios (Table 2, Fig. 1). The three model-

Table 2 Projected levels of risk for 17 European tree and shrub species for 1995 and 2095 using six risk measures (I–VI)

Species	Period/ scenario	Risk measure						Species	Period/ scenario	Risk measure					
		I	II	III	IV	V	VI			I	II	III	IV	V	VI
<i>Abies alba</i>	1995	-63	-75	76	77	-0.19	-0.02	<i>Larix decidua</i>	1995	-57	-71	39	371	-0.15	-0.01
	2095 B1	-99	-100	1575	963	-0.48	-0.10		2095 B1	-99	-100	1391	813	-0.31	-0.02
	2095 A1FI	-99	-100	1389	907	-0.53	-0.05		2095 A1FI	-96	-100	1470	903	-0.36	-0.01
<i>Betula nana</i>	1995	-5	-8	2	-9	-0.03	-0.01	<i>Picea abies</i>	1995	-22	-22	6	-24	-0.14	-0.06
	2095 B1	-37	-37	55	-57	-0.21	-0.04		2095 B1	-69	-69	129	-3	-0.47	-0.14
	2095 A1FI	-61	-67	129	89	-0.49	0.01		2095 A1FI	-88	-88	422	44	-0.61	-0.10
<i>Betula pendula</i>	1995	-7	-8	2	-15	-0.04	-0.03	<i>Pinus halepensis</i>	1995	57	-2	1	18	0.09	0.05
	2095 B1	-46	-51	46	32	-0.36	-0.03		2095 B1	303	-6	1	389	0.16	0.30
	2095 A1FI	-70	-77	202	155	-0.58	0.48		2095 A1FI	450	-34	8	621	0.00	0.48
<i>Betula pubescens</i>	1995	-5	-6	1	-12	-0.04	-0.04	<i>Pinus sylvestris</i>	1995	-3	-4	0	-3	-0.05	-0.01
	2095 B1	-57	-57	73	1	-0.37	-0.13		2095 B1	-47	-48	38	-20	-0.24	-0.10
	2095 A1FI	-77	-77	315	54	-0.59	-0.26		2095 A1FI	-72	-73	182	22	-0.46	-0.17
<i>Castanea sativa</i>	1995	19	-12	6	18	0.00	0.06	<i>Quercus coccifera</i>	1995	15	0	0	6	0.05	0.03
	2095 B1	-7	-64	101	72	-0.26	0.10		2095 B1	160	-1	-1	270	0.07	0.23
	2095 A1FI	-38	-88	361	507	-0.49	0.12		2095 A1FI	256	-15	4	426	-0.08	0.40
<i>Fagus sylvatica</i>	1995	0	-22	15	16	-0.08	0.06	<i>Quercus ilex</i>	1995	54	-1	0	69	0.15	0.09
	2095 B1	-83	-90	232	38	-0.56	0.02		2095 B1	250	-1	-1	492	0.24	0.46
	2095 A1FI	-92	-99	534	538	-0.73	0.04		2095 A1FI	320	-3	1	709	0.26	0.71
<i>Ilex aquifolium</i>	1995	22	-5	0	30	0.05	0.08	<i>Quercus pubescens</i>	1995	11	-17	7	16	-0.02	0.04
	2095 B1	60	-18	6	207	0.01	0.25		2095 B1	42	-49	53	70	-0.23	0.15
	2095 A1FI	75	-27	16	331	-0.08	0.41		2095 A1FI	3	-94	253	390	-0.51	0.18
<i>Juniperus communis</i>	1995	4	-1	0	5	0.03	0.02	<i>Quercus robur</i>	1995	7	-1	0	24	0.01	0.07
	2095 B1	-5	-8	1	-20	-0.03	-0.03		2095 B1	-1	-17	5	75	-0.11	0.23
	2095 A1FI	-22	-23	11	-51	-0.12	-0.16		2095 A1FI	-13	-40	26	211	-0.29	0.46
<i>Juniperus oxycedrus</i>	1995	36	-10	1	34	0.03	0.06								
	2095 B1	229	-55	17	438	-0.17	0.34								
	2095 A1FI	179	-97	114	778	-0.44	0.36								

Predictions are made using generalized additive models (GAMs) and are based on HadCM3 climate model data for the least (B1) and most (A1FI) severe emission scenario. Risk measures: I = % change in climatically suitable area (full dispersal) since 1945, II = % change in climatically suitable area (no dispersal) since 1945, III = change in average distance [km] from suitable cell in 1945 to nearest suitable cell in later periods, IV = change in average distance (km) from suitable cell in 1945 to all suitable cells in later periods, V = change in average climatic suitability of cells already occupied in 1945, VI = change in average climatic suitability of cells unoccupied in 1945. Results for 2045 are shown in Appendix S1.

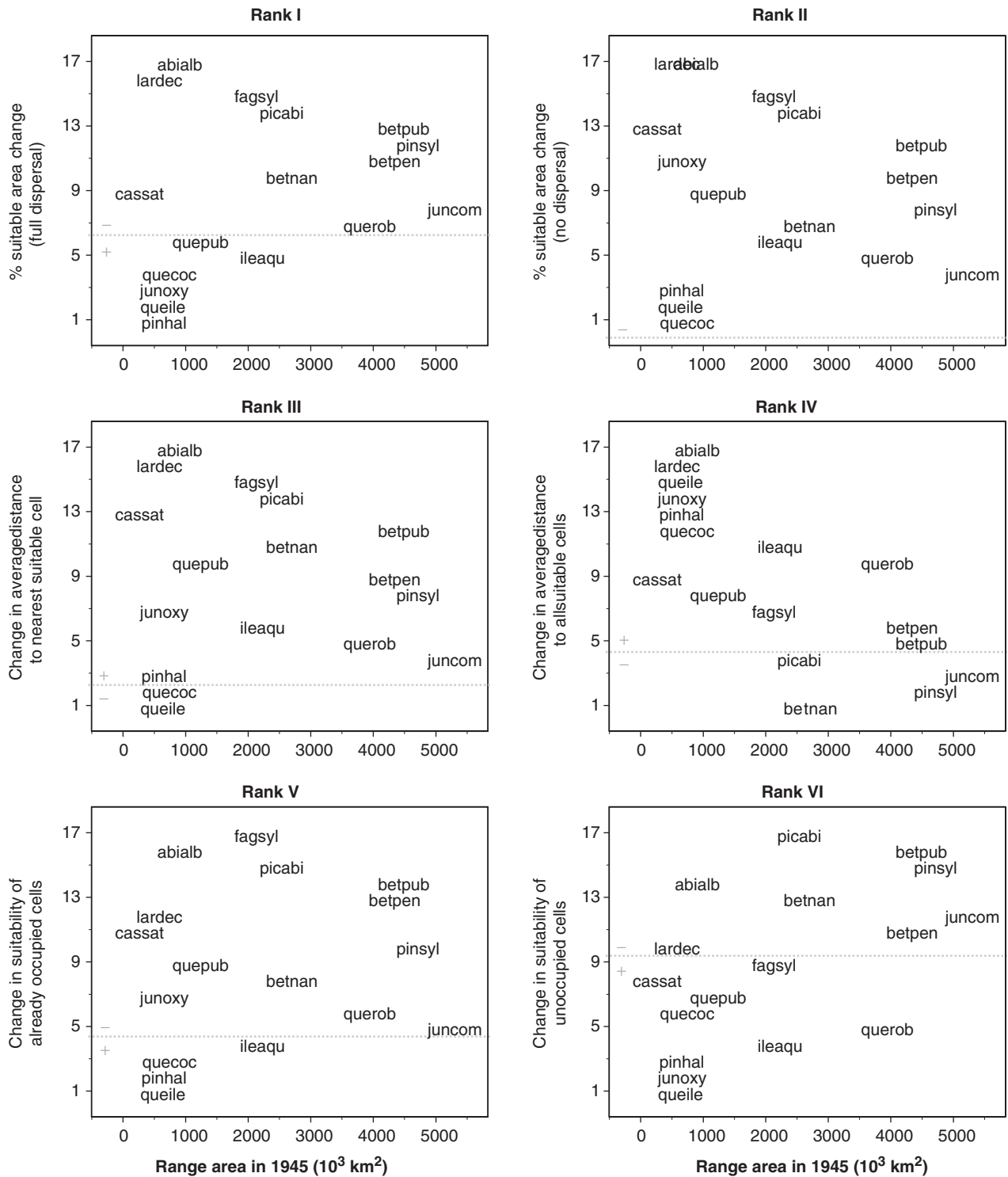


Fig. 1 Relationship between observed range area in 1945 (x-axis) and risk status of 17 European tree and shrub species ranked according to the projected level of extinction risk in 2095 using six different risk measures (I–VI) for HadCM3 climate model, low emission scenario B1. Modelling method: generalized additive models: 1, lowest risk; 17, highest risk. I = % change in climatically suitable area (full dispersal) since 1945, II = % change in climatically suitable area (no dispersal) since 1945, III = change in average distance from suitable cell in 1945 to nearest suitable cell in 2095, IV = change in average distance from suitable cell in 1945 to all suitable cells in 2095, V = change in average climatic suitability of cells already occupied in 1945, VI = change in average climatic suitability of cells unoccupied in 1945.

Table 3 Agreement between the three modelling methods generalized additive models (GAMs), generalized linear models (GLMs), classification trees (CTs) in assessing the rank (1 = lowest risk, 17 = highest risk) assigned to each species based on the six risk measures (I–VI)

	Risk	Measure	GAM	GLM	CT
GAM	I	Change in suitable area (full dispersal)	1	0.716**	0.767**
	II	Change in suitable area (null dispersal)	1	0.488*	0.592*
	III	Change in distance to nearest suitable cell	1	0.289	0.632**
	IV	Change in distance to all suitable cells	1	0.718**	0.806**
	V	Change in suitability of already occupied cells	1	0.451	0.632**
	VI	Change in suitability of unoccupied cells	1	0.782**	0.777**
GLM	I	Change in suitable area (full dispersal)		1	0.865**
	II	Change in suitable area (null dispersal)		1	0.440
	III	Change in distance to nearest suitable cell		1	0.630**
	IV	Change in distance to all suitable cells		1	0.721**
	V	Change in suitability of already occupied cells		1	0.439
	VI	Change in suitability of unoccupied cells		1	0.797**
CT	I	Change in suitable area (full dispersal)			1
	II	Change in suitable area (null dispersal)			1
	III	Change in distance to nearest suitable cell			1
	IV	Change in distance to all suitable cells			1
	V	Change in suitability of already occupied cells			1
	VI	Change in suitability of unoccupied cells			1

Spearman's ρ rank correlation coefficient of risk ranks between the three different modelling methods using B1 scenario conditions in 2095.

** $P < 0.01$; * $P < 0.05$ ($n = 17$, two tailed).

Table 4 Relationship between the six risk measures (I–VI) shown as correlation (Spearman's ρ) between ranks assigned to each species by the six different measures of risk (I–VI) using three different modelling methods for B1 2095 conditions

			Risk I	Risk II	Risk III	Risk IV	Risk V	Risk VI
Risk I	Change in suitable area (full dispersal)	GAM	1	0.815**	0.877**	−0.233	0.904**	0.816**
		GLM	1	0.956**	0.917**	−0.723**	0.958**	0.843**
		CT	1	0.478	0.718**	−0.691**	0.630**	0.728**
Risk II	Change in suitable area (no dispersal)	GAM		1	0.955**	0.058	0.907**	0.510*
		GLM		1	0.885**	−0.656**	0.936**	0.813**
		CT		1	0.775**	−0.088	0.885**	0.650**
Risk III	Change in distance to nearest suitable cell	GAM			1	−0.071	0.917**	0.625**
		GLM			1	−0.652**	0.877**	0.853**
		CT			1	−0.319	0.775**	0.743**
Risk IV	Change in distance to all suitable cells	GAM				1	−0.228	−0.605*
		GLM				1	−0.821**	−0.831**
		CT				1	−0.235	−0.551*
Risk V	Change in suitability of already occupied cells	GAM					1	0.716**
		GLM					1	0.865**
		CT					1	0.713**
Risk VI	Change in suitability of unoccupied cells	GAM						1
		GLM						1
		CT						1

** $P < 0.01$; * $P < 0.05$ ($n = 17$, two tailed). See Table 2 for explanation of the six risk measures.

GAMs, generalized additive models; GLMs, generalized linear models; CTs, classification trees.

ling methods show only moderate agreement in the ranking of the species when using this measure (Table 3). With all three methods, there is generally a significantly positive relationship between measure II and all other measures apart from measure IV (change in distance to all climatically suitable cells) for which there is no, or a negative, relationship (Table 4).

Risk from changes in distance to climatically suitable areas

Risk measures III and IV quantify the risk a species is likely to face due to changes in projected distances to climatically suitable areas. Using measure III (average distance from any cell suitable in 1945 to the nearest cell suitable in later periods), *Quercus ilex* and *Q. coccifera* are predicted to have the smallest risk with the average distance to the nearest suitable cells being ca. 1 km less in 2095 (B1 scenario) than in 1945 (Table 2, Fig. 1). For all other species, the distance to the nearest cell with suitable climate conditions is predicted to increase, and is greatest for *A. alba* with >1500 km (Table 2).

For the lowest-risk species *Betula nana*, the average distance to all climatically suitable cells (measure IV) is predicted to be on average 57 km smaller by 2095 under the B1 scenario and 89 km further away under the A1FI scenario (Table 2). For the highest-risk species *A. alba*, this distance is predicted to increase by 963 km under the B1 scenario and by over 907 km under the A1FI scenario (Table 2). Generally, the risk from changes in the average distance to all cells with suitable climate conditions (measure IV) is lower for species with large range areas in 1945 and all species characteristic for Mediterranean biomes face a high risk using this measure (Fig. 1). There is a significantly positive relationship ($P < 0.01$) between the risk rank order assigned to the species by the different modelling methods when using the distance measures III and IV, with the exception of the rank order given using GLMs and GAMs for measure III where the relationship between the two methods is positive but not significant (Table 3). For all methods, the average distance to the nearest suitable cell (measure III) is significantly positively correlated with all other measures except measure VI with which the relationship is generally negative (Table 4). The average distance to all suitable cells (measure IV) on the other hand, shows an often significant, negative relationship with all other risk measures.

Risk from changes in climatic suitability

Risk measures V and VI quantify the risk a species is likely to face due to changes in climatic suitability in presently occupied and in presently unoccupied cells

without applying cut-off levels for the predicted species distributions in the post-1945 periods. Conditions at locations modelled suitable in 1945 become most favourable (lowest risk) for the Mediterranean species *Q. ilex* under the B1 and the A1FI scenario by 2095 with an average increase in probability of occurrence of 0.24 and 0.26, respectively (measure V – Table 2). For 13 out of 17 species, however, conditions are predicted to become less suitable. The highest-risk species, *Fagus sylvatica*, shows an average decrease in probability of occurrence of 0.56 and 0.76 under the B1 and A1FI scenarios (Fig. 1, Table 2).

Conditions at locations at which the species were not predicted to be present in the 1945 (measure VI) show the highest increase in suitability (lowest risk) for *Q. ilex* by 2095 with an average increase in probability of occurrence of 0.46 and 0.71 for the B1 and A1FI scenario (Table 2). The largest decrease in climate suitability of these cells (highest risk) is predicted for *P. abies* with an average decrease of 0.14 for the B1 scenario and for *Pinus sylvestris* with an average decrease of 0.17 for the A1FI scenario (Fig. 1, Table 2). Risk measure V shows a positive but not significant relationship between modelling methods, whereas measure VI showed significantly positive relationship indicating higher agreement between modelling methods for the latter measure (Table 3). Both risk measures V and VI are positively correlated with other measures of risk, except for with measure IV, with which they are negatively correlated (Table 4).

Discussion

Methodological limitations and artefacts

The measures of risk presented here are based on modelled projections of the spatial arrangements of suitable climate space using bioclimatic models. Such projections are prone to a number of sources of uncertainties and the results presented here should therefore be viewed in the light of the following four main considerations: the choice of climate model, the choice of distribution modelling methods, mathematical artefacts, and human interference.

All projections used for the present analyses are based on the HadCM3 global climate model and the most moderate and the most extreme emission scenarios B1 and A1FI. For other climate models, the projected spatial distribution of future climate conditions may be different from the conditions projected by the HadCM3 model. The HadCM3 climate model was selected here as one of the models that predicts average changes in temperature and precipitation among the set of climatic models considered by the IPCC (IPCC, 2001). Using

different climate models may have changed the magnitude but not the direction (increase vs. decrease) of the modelled area and distance effects (see Ohlemüller *et al.*, 2006).

The choice of distribution modelling method can have some effect on the outcome of projected species distributions (e.g. Thuiller *et al.*, 2004; Araújo *et al.*, 2005). We, therefore, complemented our results obtained using GAMs with two additional modelling methods: GLMs and CTs. Our results suggest that the risk ranks assigned to our set of species is, in the majority of cases, in agreement between different modelling methods (Tables 3 and 4). However, for some cases, GLMs and CTs resulted in a different ranking of species than those obtained using GAMs. In these cases, a consensus analysis of several modelling methods might be necessary to reduce uncertainty in the risk assessments based on the projected range shifts (Araújo *et al.*, 2005). Furthermore, some of the model accuracies reported here may be artificially inflated due to spatial autocorrelation in both species and the climate data.

Some of the relationships between range size, risk rank, and between the risk measures are likely to be to some extent the result of mathematical artefacts (McPherson *et al.*, 2004). For instance, if the climatically suitable area of a species is predicted to shrink towards its core (i.e. high-risk rank), the average distance between suitable cells should also decrease (i.e. low-risk rank) out of mathematical necessity (compare significant negative correlations between risk measures I and IV in Table 4). If a species is predicted to lose large areas of climatically suitable conditions, it is likely that these areas will show a strong decline in climatic suitability (compare significant positive correlations between risk measures II and V in Table 4). However, the magnitude of these effects as well as exceptions provide valuable information that can help to refine the risk status of a species. High risk has been assigned to European boreal species based on losses of suitable climate space under the full dispersal scenario in this and other studies (e.g. Thuiller *et al.*, 2005b). However, it is very likely that this is at least to some extent a result of artificially truncating the study area in eastern Europe (Ohlemüller *et al.*, 2006). There will most likely be large areas of suitable climate for these species in the topographically uniform areas of Eurasia just to the east of our study area (see e.g. Huntley *et al.* (1995) and Sykes & Prentice (1995) for *P. abies* and *P. sylvestris*).

Human influence can lead to a lack of equilibrium between species distributions and climate and currently observed distributions might only partially reflect the potential distributions of the species. This in turn affects the parameterization and outcomes of the bioclimatic models, although this might be less of a problem at

coarse resolutions and large scales, as used here. Alternative methods avoiding the 'lack of equilibrium'-problem are individual- and process-based models. Although rapid progress is made, these models often ignore interspecific competition and community effects and therefore tend to predict the fundamental rather than the realized niche space of a species. Until further progress is made in improving bioclimatic models by incorporating ecologically relevant physiological, dispersal, and competition parameters, the outcomes of future projections of species distributions in human-dominated landscapes have to be interpreted with caution. However, we are confident that at least the direction of effects can be inferred from the currently used methods as described here.

Different measures of risk and species prioritization

Attempts to assess and prioritize species in terms of the risk they are likely to face under future climate change is currently largely based on assessment of changes in projected shifts in range size or climatically suitable area (e.g. Bakkenes *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005b). In our study, different measures of risk often resulted in different ranking and prioritization of species according to the projected risk (illustrated in Fig. 1 for 2095 using the moderate B1 scenario and projected distributions derived from GAMs). The boreal and temperate species *A. alba*, *P. abies*, *L. decidua* and *F. sylvatica* are predicted to face the highest risk due to loss in climatically suitable area both under full and no dispersal scenario (Fig. 1). All are predicted to lose more than two-thirds of their area occupied in 1945. This GAM-derived ranking is consistent with the results of the other two modelling methods, although *F. sylvatica* generally is assigned a lower risk when using a GLM or CT to predict its distribution than when using a GAM (see Appendix S2). The change in average distance to the remaining climatically suitable area is predicted to be considerably smaller for *P. abies* and for *F. sylvatica* (−3 and +38 km) than for *L. decidua* and *A. alba* (+813 and +963 km) (Table 2). This arises because the latter two species are presently mainly found in central European alpine regions but most of their future climatically suitable area is predicted to be in northern Europe, implying additional potential risk for these two species. Together with improved estimates of dispersal kernels of these species, such information can improve ecological risk assessment under climate change (Hulme, 2005). The recognition of a specific type of risk means that it should be taken into consideration, but not that it will necessarily prove catastrophic for a given species. For *L. decidua* and *A. alba*, dispersal limitation may not be a

major concern, given that both species are already widely planted in northern Europe.

Species from southern European evergreen forest and dry woodlands (*P. halepensis*, *Q. coccifera*, *Q. ilex*, and *Juniperus oxycedrus*) are likely to gain large areas of climatically suitable area by 2095 and are accordingly considered as low risk under this criterion (Fig. 1, Table 2). This is consistent among the three modelling methods (see Appendix S2). Also, for these species, climatic conditions will generally improve both inside and outside presently occupied areas (Table 2, Fig. 1). This corroborates the findings of other studies which found that Mediterranean areas are generally expected to experience smaller risks from loss in climatically suitable areas under climate change (e.g. Thuiller *et al.*, 2005a,b). However, our analyses indicate that Mediterranean species are likely to face difficulties in terms of the distance they have to cover in order to reach future suitable climates (Fig. 1). For *Q. ilex*, the average distance from any presently occupied cells to all other suitable cells is predicted to be 492 km further away for *Q. ilex* in 2095 than it is now under the moderate B1 emission scenario (risk measure IV – Table 2). European jays, one of the main dispersal agent for *Q. ilex*, will carry acorns on average 250 m away from a mother tree with dispersal distances increasing with increasing habitat heterogeneity (Gómez, 2003). Given that the average distance to the nearest suitable cell for *Q. ilex* will be shorter in 2095 than it is at present (risk measure III – Table 2), this species should be able to keep up with future shifting suitable climate space, at least at the establishment stage of its life cycle and in close neighbourhood to existing populations. However, it is unlikely that *Q. ilex* will be able to reach and occupy the entire area of projected future suitable climate space for some considerable time, given the large average distance to all cells climatically suitable in the future.

Our data illustrate how xerophytic and evergreen species would have been given low conservation priority because of the apparently small risk of losing climatically suitable area, but higher conservation priority when considering distances to climatically suitable areas. The ability of a species to persist in an area following changes in environmental conditions is not only determined by local site conditions but also by its dispersal capacity (e.g. Pausas & Lavorel, 2003); quantifying the latter in the context of bioclimatic models can, therefore, add important information to species prioritization analyses under climate change. Utilizing additional information on distance to suitable climates and on shifts in climatic suitability, together with already existing measures of areas changes, can help to prioritize current and new target species and areas for conservation (e.g. Pyke *et al.*, 2005).

Range size and risk status

We found no consistent relationship between present-day range size and the risk status of the 17 investigated European tree and shrub species (Fig. 1, Appendix S2). Of the species with a smaller range size ($<1000 \times 10^3 \text{ km}^2$), Mediterranean species are predicted to generally face a lower risk than all other species from central and northern Europe for five out of the six risk measures used here (Fig. 1). Species of xerophytic shrubland and evergreen forests of warm and dry southern European regions generally have smaller range sizes. They will in the future have extensive areas of suitable climates outside their current range (Thuiller *et al.*, 2005b) and these new areas will generally be very suitable (Table 2, Fig. 1). However, these species face a higher risk than most other species due to the fact that future climatically suitable areas will be further away than at present. Not only will suitable areas be further away than for species of colder climates, but the mountainous and heterogeneous topography of southern Europe can further prevent Mediterranean species from filling up their potentially suitable climate space (Svenning & Skov, 2004).

Species with large range sizes ($>4000 \times 10^3 \text{ km}^2$), such *Juniperus communis*, *P. sylvestris*, *Betula pubescens*, *B. pendula*, and *Quercus robur*, are predicted to be most negatively affected by loss of climatically suitable areas under the full dispersal criterion and by low climatic suitability of locations outside their current range (Fig. 1). Widespread species are predicted to lose less of their already occupied area than more restricted species (Fig. 1, Table 2), probably due to their wider tolerance ranges (Thuiller *et al.*, 2005b). Many of these species will lose climatically suitable area, mostly in western parts of Europe, and their suitable climate space is predicted to shift northwards (Sykes & Prentice, 1996). The Arctic Ocean to the north of Europe limits their expansion, causing these species to lose relatively more climatically suitable area under the full dispersal scenario than species from southern Europe (Huntley *et al.*, 1995).

Range shifts of woody species in response to recent climate change can already be observed in the field (e.g. Walther *et al.*, 2005). Validating projected range shifts with field observations is therefore crucial for a successful implementation of risk assessments based on such projections. To this end, it would be highly beneficial to establish long-term monitoring sites across Europe covering the entire European climate space. Intensive monitoring would not only allow us to analyse species performance across geographic and climatic ranges but also to track already occurring and predicted range shifts at both ends of a species' range. Such information is currently still scarce but would greatly improve our understanding of the process and tempo of range shifts.

Conclusions

Assessing the risk species will face under future climate change solely on the basis of changes in area of suitable climate may give an incomplete picture of the true threats. We provide examples of other measures of risk based on distance to climatically suitable areas and on degrees of suitability in already occupied and new cells. In applying these measures to European tree species, we were able to identify different aspects of risk for different species. Losing large areas of climatically suitable area is worse for a species for which the remaining areas of suitable climate in the future will be far away than for a species for which such areas will be nearby. Likewise, losing large areas of suitable climates is likely to pose a bigger threat for species for which the remaining areas which it already occupies become very marginal in terms of climate suitability than for species for which these remaining areas will increase in climatic suitability. Including such additional information has the potential to refine and add ecologically meaningful parameters to climate change risk assessments based on bioclimatic models.

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Supplementary material

The following supplementary material is available online from www.Blackwell-Synergy.com

Appendix S1. Projected extinction risk for 17 European tree and shrub species for three time periods (1995, 2045 and 2095) using six risk measures (I–VI). Predictions are made using generalized additive models (GAMs) and are based on HadCM3 climate model data for the least (B1) and most (A1FI) severe emission scenario. See Table 2 for detailed description of risk measures.

Appendix S2. Relationship between observed range area in 1945 (x-axis) and risk status using two alternative modelling methods: (a) GLMs, (b) classification trees (CT). See Fig. 1 for details.