Vulnerability of dynamic genetic conservation units of forest trees in Europe to climate change

SILVIO SCHUELER[1], WOLFGANG FALK[2], JARKKO KOSKELA[3], FRANÇOIS LEFÈVRE[4], MICHELE BOZZANO[3], JASON HUBERT[5], HOJKA KRAIGHER[6], ROMAN LONGAUER[7] and DITTE C. OLRIK[8]

[1]*Department of Genetics, Federal Research and Training Centre for Forests, Natural Hazards and Landscapes, Hauptstr. 7, Vienna 1140, Austria,* [2]*Bavarian State Institute of Forestry, Hans-Carl-von-Carlowitz-Platz 1, Freising 85354, Germany,* [3]*Bioversity International, Via dei Tre Denari 472/a, Maccarese (Rome) 00057, Italy,* [4]*UR629 Ecologie des Forêts Méditerranéennes URFM, INRA, Domaine St Paul Site Agroparc, Avignon 84914, France,* [5]*Northern Research Station, Forest Research, Midlothian, Roslin EH25 9SY, United Kingdom,* [6]*Slovenian Forestry Institute, Večna pot 2, Ljubljana 1000, Slovenia,* [7]*National Forest Centre, T.G. Masaryka 24, Zvolen 960 92, Slovakia,* [8]*Danish Ministry of the Environment, Nature Agency, Gillelejevej 2B, Græsted 3230, Denmark*

Abstract

A transnational network of genetic conservation units for forest trees was recently documented in Europe aiming at the conservation of evolutionary processes and the adaptive potential of natural or man-made tree populations. In this study, we quantified the vulnerability of individual conservation units and the whole network to climate change using climate favourability models and the estimated velocity of climate change. Compared to the overall climate niche of the analysed target species populations at the warm and dry end of the species niche are underrepresented in the network. However, by 2100, target species in 33–65 % of conservation units, mostly located in southern Europe, will be at the limit or outside the species' current climatic niche as demonstrated by favourabilities below required model sensitivities of 95%. The highest average decrease in favourabilities throughout the network can be expected for coniferous trees although they are mainly occurring within units in mountainous landscapes for which we estimated lower velocities of change. Generally, the species-specific estimates of favourabilities showed only low correlations to the velocity of climate change in individual units, indicating that both vulnerability measures should be considered for climate risk analysis. The variation in favourabilities among target species within the same conservation units is expected to increase with climate change and will likely require a prioritization among co-occurring species. The present results suggest that there is a strong need to intensify monitoring efforts and to develop additional conservation measures for populations in the most vulnerable units. Also, our results call for continued transnational actions for genetic conservation of European forest trees, including the establishment of dynamic conservation populations outside the current species distribution ranges within European assisted migration schemes.

Keywords: climate niche modelling, favourability function, forest genetic resources, gap analysis, genetic conservation unit, velocity of climate change

Received 22 July 2013; revised version received 6 November 2013 and accepted 8 November 2013

Introduction

A large proportion of terrestrial ecosystems are dominated and shaped by forest trees, which provide the setting for huge numbers of associated organisms and guaranty ecosystem functioning, carbon storage (Pan *et al.*, 2011), and various benefits for the human population, including recreation and wood production (Hanewinkel *et al.*, 2012). Since climate conditions are considered to be a major determinant of tree species' distribution ranges (e.g., Woodward, 1990; Sykes *et al.*, 1996; Randin *et al.*, 2013), anthropogenic climate

change is expected to modify the distribution of tree species, tree species diversity and the forest ecosystems connected to these species within a few tree generations (Walther *et al.*, 2002; Thuiller *et al.*, 2006; Morin *et al.*, 2008). Generally, trees have developed evolutionary means to facilitate migration and adaptation. For example, trees possess large genetic variation within populations and less differentiation among populations as compared to other plants (Hamrick *et al.*, 1992; Hamrick & Godt, 1996; Alberto *et al.*, 2013). Trees also exhibit strong and extensive gene flow even over long distances (Schueler & Schlünzen, 2006; Buschbom *et al.*, 2011; Robledo-Arnuncio, 2011) and this helps to spread genotypes that are advantageous in new climates (Kremer *et al.*, 2012). Nevertheless, the

Correspondence: Silvio Schueler, tel. +43 0 187838 2228, fax +43 0 187838 2250, e-mail: silvio.schueler@bfw.gv.at

current speed of climate change is expected to create serious migration and adaptation lags for many trees (e.g., Savolainen *et al.*, 2007; Kuparinen *et al.*, 2010; Nathan *et al.*, 2011) and to cause the extinction of local populations in particular if they are small and located at the rear edge of species distributions (Hampe & Petit, 2005; Aitken *et al.*, 2008). Moreover, tree species exhibit numerous local adaptations to their present habitats that are likely to be altered as a result of climate change. Such local adaptations are a product of diversifying selection in heterogeneous environments and they are found for numerous phenotypic traits on the juvenile and the adult phase of many species (e.g., Hurme *et al.*, 1997; Hannerz *et al.*, 1999; Rehfeldt *et al.*, 2002; Alberto *et al.*, 2013). Under a rapidly changing climate, these adaptations are considered to be a serious load because local populations will be maladapted to future conditions (St. Clair & Howe, 2007). Nevertheless, local adaptations also represent valuable genetic resources for the long-term survival of the species and allow forest management to undertake active adaptation measures in order to cope with climate change.

The maintenance of evolutionary processes within tree populations has long been the main goal of genetic conservation of forest trees (Ledig, 1986; Eriksson *et al.*, 1993; Namkoong, 1997). The dynamic conservation approach safeguards the potential of tree populations for continuous adaptation and it is mainly practiced through *in situ* conservation, i.e. managing tree populations at their natural sites within the environment to which they are adapted to. However, *ex situ* conservation can also be dynamic in cases of artificial but dynamically evolving tree populations. In Europe, a set of minimum requirements was recently developed for the dynamic conservation units of forest trees (Koskela *et al.*, 2013) and all those units in different countries that meet these requirements have been documented in the EUFGIS Portal (http://portal.eufgis.org). These units are natural (*in situ*) or artificially established (both *in situ* and *ex situ*) tree populations that are specifically managed, with silvicultural interventions as needed, for maintaining evolutionary processes and adaptive potential in the long term (i.e. across tree generations). Each unit has a designated status (legal or other arrangements) at the national level and one or more tree species identified as target species for long-term genetic conservation. Currently documented in 31 countries, these units form a pan-European network for dynamic conservation of forest genetic resources. As a whole, this conservation network covers very different environmental zones in Europe though a more detailed insight has revealed significant gaps at the level of species' distribution ranges (Lefèvre *et al.*, 2013).

The European network of the genetic conservation units for forest trees is an example of a dynamic and large-scale conservation approach, which is essential for adapting conservation systems to climate change (Hannah, 2010). From the conservation planning point of view, however, it is crucial not only to identify gaps but also assess the vulnerability of such conservation systems to climate change and explore ways to make them more resilient. For this purpose, the necessary first step is the identification of those genetic conservation units which are located at the existing climatic limit of species' distribution ranges and which are thus most susceptible to climate change. This information would help deciding which units should be monitored and managed more carefully. Furthermore, it would be also useful for refining conservation strategies, i.e. to consider if some units should be targeted for complementary *ex situ* conservation in seed banks or field collection, and whether artificial conservation units should be established for a tree species outside its current distribution range due to climate change.

The evaluation of conservation efforts and the incorporation of climate change considerations into conservation strategies and measures require information not only on the local rate of climate change but also on species climatic niches as well as the climatic conditions of individual units and the whole network (Box 1). In order to understand the climate-related risk for a single species within the conservation network, the representation within the network needs to be related to the species' climate niches (Hutchinson, 1957; Holt, 2009). In recent years, species distribution models have been successfully applied to better describe the climate niche of species (Sykes *et al.*, 1996; Thuiller *et al.*, 2006; Higgins *et al.*, 2012) and to evaluate conservation measures on regional and global scales (Araújo *et al.*, 2011; Game *et al.*, 2011; Summers *et al.*, 2012). However, current species distribution models only rarely consider intraspecific variation or well-documented local adaptations of species (D'Amen *et al.*, 2012). This is mainly because phenotypic variation and its correlation with climate conditions have been analysed only for a very few tree species and seldom over species complete distribution ranges. In particular, local adaptations at the climatic edges of species' ranges or in outlier populations are underestimated and species occurrences are misclassified with current models (Gavin & Hu, 2006). This happens because necessary statistical thresholds may remove outlier occurrences in order to avoid false positive predictions (Liu *et al.*, 2005). Therefore, the evaluation of a large-scale conservation network should take advantage of relaxed model assumptions and weight conservation areas according to their relative climate risk instead of absolute risk measures. In addition to a

Box 1

Schematic illustration of the potential threats to populations within the genetic conservation units as analysed within the present study. As populations are adapted to their local environments, they usually have a smaller climatic niche than the species in general. The favourabilities F_{curr} and F_{fut} indicate the relation of a given population to the species overall niche under current and future conditions. The niche displacement distance ΔF specifies the expected change in favourability for a single population. Even if the future environment of a local population (e.g., Pop1) is within the species total niche, the favourability change might be too large to allow local adaptation. Populations that occur at the edge of the climate niche already today (e.g., Pop2) might live far outside the species niche in the future. Since climate niche models were not available for all species in the network (e.g., rare species), we also calculated the spatial velocity of climate change per year according to Loarie *et al.* (2009). This measure relates the expected temperature change to the environmental heterogeneity of the respective landscape and is a useful measure for a general assessment of the units irrespective of the target species within conservation units.
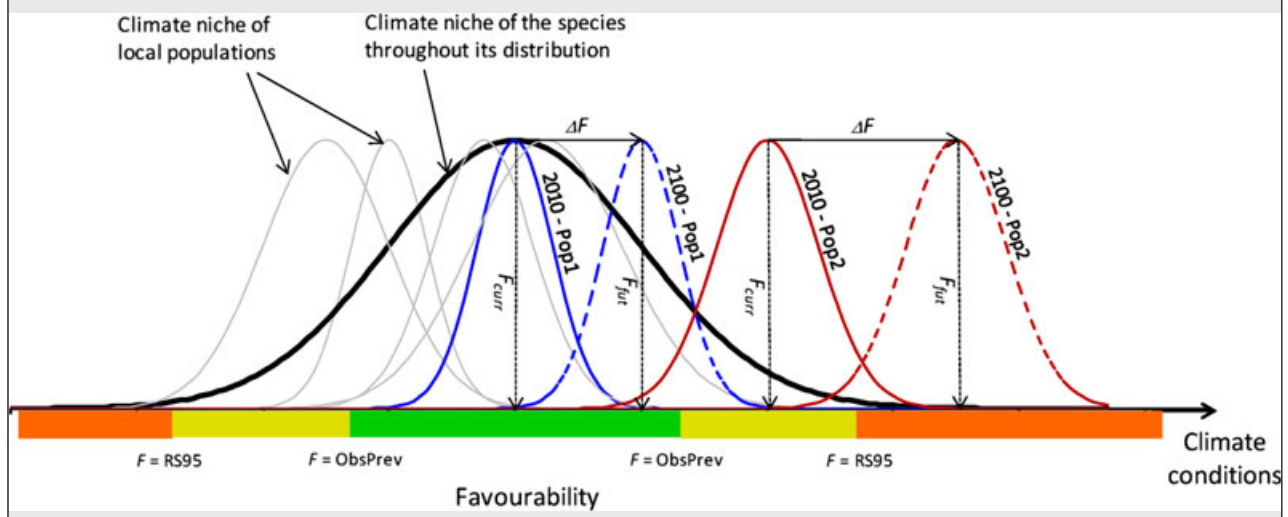
species-specific risk assessment, the velocity of the environmental change at a specific conservation unit is expected to be an indicator for putative maladaptations of local populations. A promising approach to relate the extent of climate change to the characteristics of specific landscapes and conservation areas was proposed by Loarie *et al.* (2009). Their approach is based on the assumption that more heterogeneous environments harbour higher numbers of climatic niches and thus they might enable species to find new suitable habitats within small spatial distances. In particular, this seems to be true for mountainous areas where strong environmental gradients can be found on small spatial scales and where migration capacity of species exceeds the geographic shift of suitable habitats (Jump *et al.*, 2009). Recently, this impact of landscape roughness on thermal variability and potential buffering to climate change was confirmed by an empirical study of plant communities and microclimatic measurements in north-western Europe (Lenoir *et al.*, 2013).

The objective of this study was to analyse the projected impact of climate change on the large-scale network of genetic conservation units of forest trees in Europe. In particular, we aimed at identifying vulnerable units and selected six target species for more detailed analyses. As part of these analyses, we assessed the vulnerability of the selected target species on the level of single conservation units and for the entire conservation network using climate niche modelling and favourability functions (e.g., Real *et al.*, 2006). In addition, for each unit the velocity of climate change was calculated following the concept of Loarie *et al.* (2009) for a general vulnerability assessment irrespective of the target species present.

Materials and methods

In order to understand the potential threats due to climate change, we performed two different analyses. Firstly, for six of the most common target tree species, the climatic conditions of the units were related to the modelled climate niche of the respective species. Applied to current and projected climate conditions, these models should help to identify in which units the target tree species are occurring outside or at the edge of their climatic niche. Secondly, we calculated the velocity of climate change for each unit following the approach of Loarie *et al.* (2009). This latter analysis should also help to

evaluate the vulnerability of multi-species conservation units and those rare species within conservation units for which no stable climate niche models are available due to missing data sets. In addition, the velocity of change should help assess the effect of landscape structure in buffering potential threats of climate change.

The data on the exact location and the target species in each unit were obtained from the EUFGIS database (http://portal.eufgis.org). The dataset included 1967 genetic conservation units located in 31 countries. The size of conservation units ranges from <1 ha to >5000 ha with a mean of 111 ha unit^{-1} covering a total of 218 328 ha (Lefèvre *et al.*, 2013). Having one or multiple target tree species, these conservation units harboured a total of 2737 populations of 86 target tree species (see Lefèvre *et al.*, 2013).

Climate data were obtained from the WorldClim database (Hijmans *et al.*, 2005) which provides 'current' (1950–2000) climatic conditions and downscaled future condition for various future periods under different climate scenarios according to the Intergovernmental Panel on Climate Change (IPCC). For the present analysis, the current conditions with a resolution of 30 arc-s were applied. For future conditions, we selected the emission scenario A1B and used the results of the global climate model MPI-Echam5 downscaled to 30 arc-s for the period of 2070–2099. The MPI-Echam5 model results were used because they provide a good average of the various models available and because the model has been rated as one of the most accurate global climate models (e.g., Connolley & Bracegirdle, 2007).

Vulnerability of target species

To estimate the potential threat of climate change to a target species within a given unit, we have to consider the species' environmental niche. In this study, we used generalized additive models (GAM) (Hastie & Tibshirani, 1990; Wood, 2006) to describe the relationship between the presence–absence of a species and its climatic limits. GAMs allow the fitting of response curves using nonparametric smoothing function instead of parametric terms. GAMs were built with the R package mgcv (Wood, 2009) as this software provides an automated choice of smooth terms (Wood, 2006). Interaction terms were not considered because the number of potential parameters to be estimated increases exponentially with the number of predictors in GAMs and would violate our intention of parsimonious model building. We focused on six target tree species for which a reasonably high number of genetic conservation units exist (>150) and for which reliable niche models could be calculated with the available presence–absence dataset. These species include the six most frequent and stand-forming European tree species, three of them coniferous, i.e. silver fir (*Abies alba*), Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and three of them deciduous, i.e. European beech (*Fagus sylvatica*), sessile oak (*Quercus petraea*) and pedunculate oak (*Quercus robur*).

The presence–absence data for the species climate niche models were obtained from the ICP Forest Programme 'Large-scale forest condition monitoring Level I' from the period 1987 to 2007 (ICP Forests, 2010) and the natural vegetation map of Europe (Bohn & Neuhäusl, 2003). These two datasets provided a total of 9534 inventory points that covered most European countries. After removing concordant location data and selecting plots from countries with a high plot density in order to fulfil a distribution along a uniform grid of 16 × 16 km, 7540 data points remained for the final analysis. Fallacious absences (Zarnetske *et al.*, 2007; Hirzel & Le Lay, 2008) were corrected using the vegetation map data; therefore expert knowledge of vegetation ecologists was included into our analysis of the tree species' climatic niche.

The GAMs were built by using the summer precipitation sum (P_678), the average temperature of the vegetation period (T_5to9), and the average temperature of the coldest month, i.e. January (T_01) as climate parameters. These parameters have a strong physiological meaning and were selected within a stepwise backward variable selection (Falk & Mellert, 2011; Mellert *et al.*, 2011) that provided a high significance for individual variables and a low correlation among variables. We restricted the number of climate variables to three in order to describe only the main climate drivers of species distribution and to create parsimonious models.

In three cases (Scots pine and the two oak species), models led to partly implausible response curves, that revealed, in contradiction to the species ecology, a low probability of presence at certain precipitation ranges despite of documented presences. Since our interest was more on potential distribution and not on exact models of the realized niche, absences within the range of implausible curves for P_678 and T_01 were reduced by random selection of 60–70% of the respective absences. This resulted in stable response curves at sites with higher precipitation. In the case of pedunculate oak, outlier presences of T_01 above of 7 °C (N = 15) were removed. Furthermore, 56 pseudoabsences above the Alpine tree line were artificially created following the regular grid in order to describe the altitudinal tree species distribution limit in high mountains. A total of 7596 data points were used in case of beech, spruce and fir. The data screening led to the use of 5835, 7243 and 6434 sites for the models of pine, sessile oak and pedunculate oak, respectively.

Plausibility of the models was checked with the help of response curves and using quality criterions of the R-package PresenceAbsence (Freeman & Moisen, 2008) with the prevalence as a threshold where necessary. The criteria, such as area under the receiver-operating curve (*AUC*), sensitivity or specificity, were compared with values of a tenfold cross-validation ('leave-one-out approach', 10 times 10 per cent of the data left out and used for validation).

The final species climate niche models were applied for the current climate data and the average projections of the period 2070–2099. The results of the obtained GAMs are given as probability of presence for each raster cell. For interpretation of raw probability values, the model output has to be transformed either into binary presence/absence predictions or into categorical indices of favourability or suitability using threshold criteria and considering the species actual preva-

lence (Liu *et al.*, 2005; Real *et al.*, 2006). The favourability of a specific conservation unit for a species has been calculated as a function of both, the species probability of presence (as obtained by the GAM) and the actual prevalence of the species using the following formula (Real *et al.*, 2006):

$$F = \frac{\frac{P}{(1-P)}}{\frac{n_1}{n_0} + \frac{P}{(1-P)}} \quad (1)$$

Here, P is the probability output of the GAM and n_1 and n_0 are the number of presences and absences, respectively, in the dataset. The incorporation of sample prevalence into the predictions of species occurrences enable direct comparisons among species and combinations of several species for defining relevant conservation areas (Estrada *et al.*, 2008). In addition to the favourabilities under current and future climate, we calculated the favourability change for each conservation unit: $\Delta F = F_{curr} - F_{fut}$. As critical thresholds for the favourability of a unit for a given species, we chose the observed prevalence (*OP*), which gives the ratio of the species occurrences within the complete set of inventory plots, and as the second one, the required sensitivity (*RS95*). At *RS95*, the model predictions cover 95% of the true presences within the dataset at the expense of the models accuracy to describe species absences. That means, only 5% of all true presences of a given species are occurring below these favourability threshold under current climate. Hence, if these occurrences are not outside the modelled distribution due to shortcomings of the models, then they are at climatically unfavourable sites with higher risk of reduced vitality or increasing insect attacks, for example. Both, *OP* and *RS95* were obtained as output of the GAM model using the R-package PresenceAbsence (Freeman & Moisen, 2008) and transformed into favourability thresholds (OP_F and $RS95_F$, respectively) according to equation 1.

Velocity of temperature change

The velocity of temperature change is an index for the horizontal temperature change (given in km yr^{-1}) calculated from the environmental heterogeneity of the respective landscape and projected temperature change for the next century (Loarie *et al.*, 2009). In the present study, we followed the approach of Loarie *et al.* (2009) and calculated the environmental heterogeneity from a 3×3 grid cell neighbourhood using the slope function (average maximum technique) of the GIS software QGIS. The basis for these calculations was the WorldClim climate data with a resolution of 30 arc-s.

Results

Vulnerability of target species using climate envelope models

In 7596 plots with presence–absence data (ICP Forests, 2010), the occurrence of the six selected tree species ranged between 14% (silver fir) and 53% (Scots pine) of the sites. Data screening led to changes of prevalence, e.g., an increase to 68 % in case of Scots pine. The models' ability to discriminate between presences and absences, expressed as the area under the receiver-operating curve (*AUC*, Fielding & Bell, 1997) of the six models, ranged between 0.84 and 0.92. The values for adjusted R^2 were between 0.27 and 0.58. The impact of the three climate parameters on the proportion of explained deviance of GAMs for single target species is shown in Suppl Fig. S1 and S2. The focus of our models is on the potential distribution, thus, sensitivity is an important measure for us. Sensitivity values range between 0.86 and 0.92 (see Table. 1). The result of the tenfold cross-validation show that the models are stable and validation with left-out-data led to comparable quality measures (e.g., see *AUC* and R^2 adjusted in Table. 1 and suppl. Fig. S3). Maps with the current and future geographic distribution are shown in Fig. 1 for sessile oak and the other five species in the electronic supplement

Table 1 Quality and thresholds of the developed climate niche models for the six selected target species given as output of the GAM and the derived thresholds of the favourability model.

Species	GAM output									Favourability	
	N	AUC	R^2	AUC_V	R^2_V	S	Sp	OP	RS95	OP_F	$RS95_F$
A. alba	7596	0.87	0.27	0.87	0.26	0.86	0.73	0.14	0.057	0.5	0.266
P. abies	7596	0.92	0.58	0.92	0.57	0.92	0.80	0.51	0.379	0.5	0.374
P. sylvestris	5835	0.90	0.53	0.90	0.52	0.92	0.73	0.68	0.548	0.5	0.360
Q. robur	6434	0.84	0.39	0.84	0.39	0.90	0.70	0.50	0.351	0.5	0.356
Q. petraea	7243	0.90	0.46	0.90	0.45	0.89	0.75	0.36	0.223	0.5	0.343
F. sylvatica	7596	0.89	0.43	0.89	0.42	0.86	0.77	0.31	0.192	0.5	0.343

N, total number of observations (presence–absences) used; *AUC*, area under curve; R^2, adjusted regression coefficient; AUC_V, mean *AUC* of a tenfold cross-validation; R^2, adjusted regression coefficient of the tenfold cross-validation; *S*, model sensitivity; *Sp*, model specificity; *OP*, observed prevalence; *RS95*, required sensitivity where the model includes 95 % of the observed presences; OP_F, threshold of the favourability model based on *OP* (consider that OP_F is by definition 0.5 (Real *et al.*, 2006)); $RS95_F$, lower threshold of the favourability model based on *RS95*.
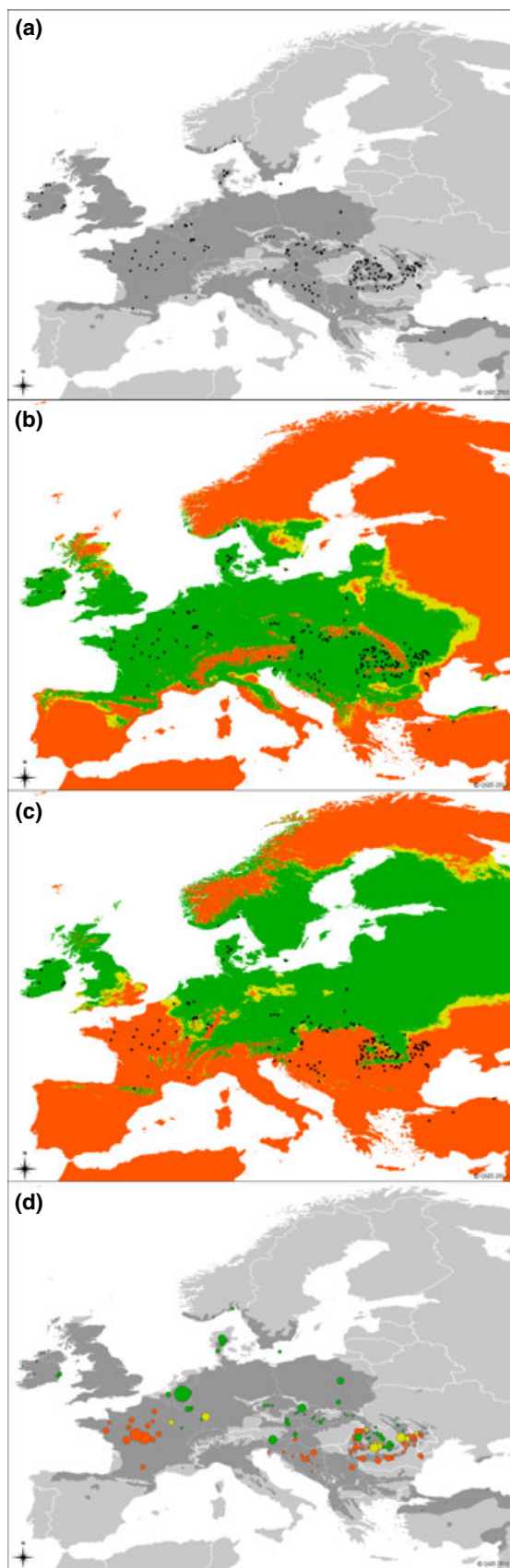
Fig. 1 Distribution and modelled favourabilities of sessile oak (*Q. petraea*) and the location of genetic conservation units (black dots) with sessile oak as target tree species: (a) natural distribution according to EUFORGEN distribution maps; (b) present and projected future (c) favourabilities *F* according to the modelled climate niche. Green: *F* > 0.5 (=observed prevalence); Yellow: 0.5 > *F* > RS95; Red: *F* < RS95. Genetic conservation units with the target species sessile oak are marked by dots. (Favourabilities of other five target species are given in the suppl Figs S2 and S3). (d) Visual summary of the whole analysis where the favourabilities are given by the same colours as above, while the velocity of change is indicated by the size of the dots (larger dots = higher velocity).

(Suppl. Fig. S4–S5). Comparing the natural distribution (Fig. 1a) with favourabilities above *RS95* under present conditions (Fig. 1b: yellow and green area) shows that the constructed model for the fundamental niche reveals a wider potential distribution than the actual realized niche today, with the exceptions of Scotland, Greece and Turkey.

In order to identify climatic gaps for certain species within the conservation network, we compared the frequency distribution of favourabilities from the conservation units with the frequency distribution of the complete species distribution baseline data, i.e. the Level-1 monitoring plots without data screening and pseudoabsences under the current climate and the future climate conditions (Fig. 2). Generally, for the six selected species, the climatic distribution of conservation units fits rather well to the respective species overall niche under current conditions (Fig. 2, left column). However, small deviations (resulting in significant differences in the G-test $p < 0.05$) can be observed at very high and low favourabilities. For pedunculate and sessile oak as well as for Norway spruce, populations with low favourabilities are underrepresented, whereas slightly higher ratios of conservation units are available for high favourabilities. Due to the high impact of vegetation period temperatures in the present models, the low and high favourabilities represent the species climatic borders, where low favourabilities correspond mainly to warm–dry conditions whereas high favourabilities represent rather cold–wet conditions. Also, units with Scots pine do not fit the species climatic niche (G-test $p < 0.05$), but in this case units at the colder end of the distribution, i.e. with higher favourabilities are underrepresented. The only species, where the current selection of units fits exactly to the climate niche is European beech (G-test $p = 0.177$).

Under future climate conditions, the favourabilities for many units, but also for many Level-1 observation plots decrease dramatically. The dashed vertical lines in Fig. 2 represent a modelled distribution limit with
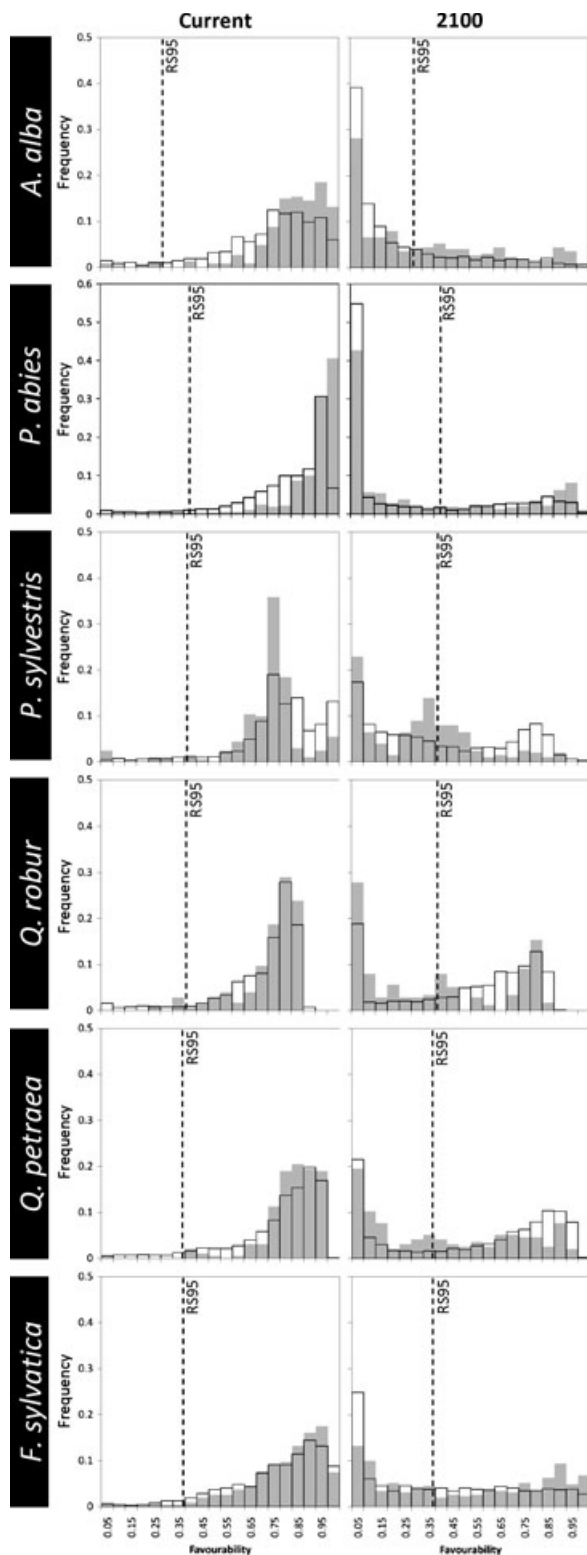
Fig. 2 Favourability of genetic conservation units (grey bars) in contrast to the favourabilities of the Forest Focus Level I occurrence data (open bars) of six selected target tree species for current and future conditions, The level I data were used as basis for the species' climate niche models.

the help of the threshold value *RS95*. Generally, the discrepancies between the species in conservation units and its natural distribution increase. The mountainous species Norway spruce, silver fir and European beech are slightly less affected in the conservation network than in its natural distribution area because a higher share of units has still favourabilities higher than *RS95*. For pedunculate oak and Scots pine, units within the highest risk-class (favourability < 0.05) are overrepresented as compared to the species distribution.

Genetic conservation units with higher favourabilities for the various species in 2100 as compared to current conditions were found only in low proportions (Suppl. Fig. S6): for the three deciduous species, the percentage of units with higher favourabilities ('winner' units) ranged from 14 to 22%, while all other units showed lower favourabilities. For coniferous trees, the situation is even more serious: here the percentage of 'winner' units ranged from to 0.5 (Scots pine) to 6% (Norway spruce). Also, the highest average decrease in favourabilities ΔF throughout the network can be expected for the three conifers, for example, the average favourability of Norway spruce populations will decrease from $F_{curr} = 0.9$ to $F_{fut} = 0.3$ (Fig. 3). For the deciduous species, the favourabilities will only decrease between 0.29 (European beech) and 0.41 (sessile oak).

Several units are being managed for genetic conservation of more than one tree species (Lefèvre *et al.*, 2013). When we compared the variation in favourabilities of different species within the same units, we found that the variation among species will increase significantly. Under current conditions, the average range of favourabilities among species within single units is 0.19, but under future conditions the average range might be more than doubled to 0.49 (Fig. 4).

Vulnerability of conservation units – velocity of climate change

Genetic conservation units within the pan-European network are expected to experience an average increase of 4.2 °C in mean annual temperature until 2100 (ranging from 1.6 °C to 5.1 °C) (Fig. S7a). Related to the environmental heterogeneity of the landscape around the units, the velocity of climate change ranges from 0.01 to 12.2 km yr^{-1} (on average 0.47 km yr^{-1} – Fig. S7b). The lowest velocity was generally found for units located in the mountainous areas of Central Europe, but also units in the Mediterranean mountains are expected to experience lower than the average speed of climate change. A comparison of the average velocity of climate change among countries confirms this trend (Fig. S8a): units in mountainous regions of Austria, Slovakia, Slovenia and Turkey, for example, are likely to be less affected by
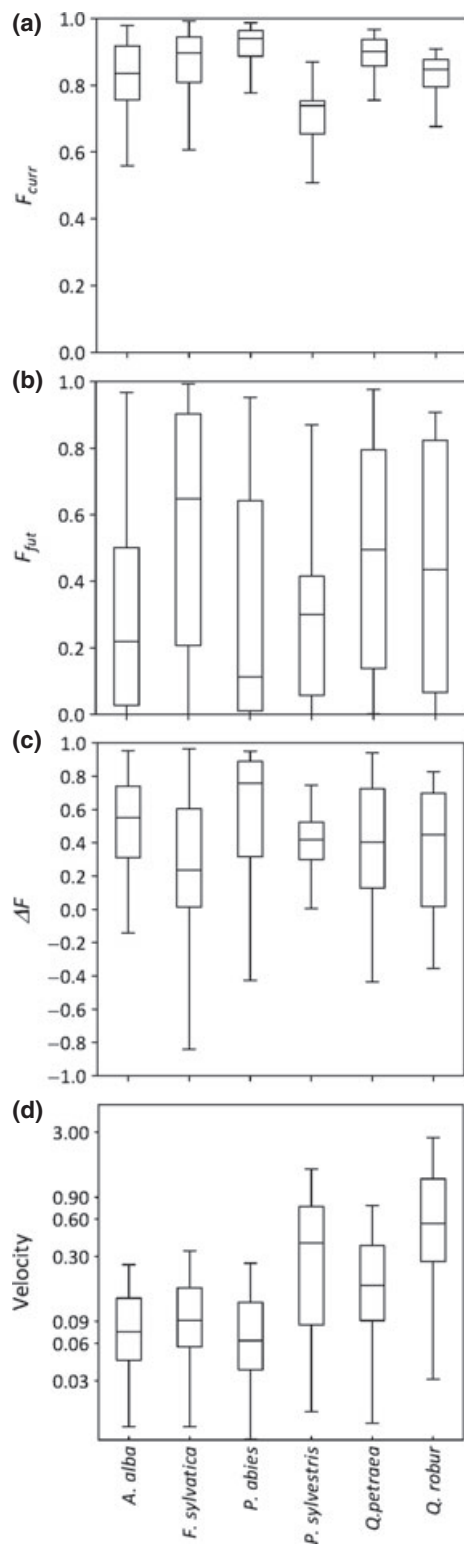
Fig. 3 Average favourabilities of six target tree species under current (a) F_{curr} and future (b) F_{fut} climate conditions as well as the favourability change (c) ΔF and the velocity of temperature change (d). Boxes mark the 25–75% quartile, whiskers the 1.5 interquartile range and the band the median.
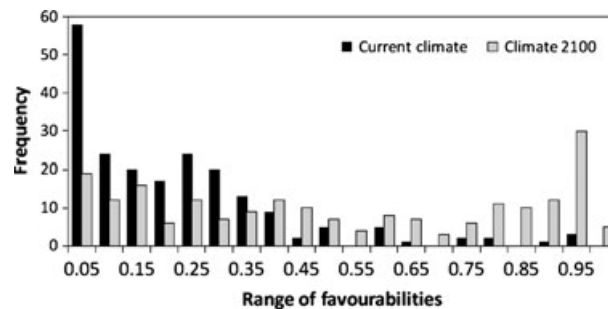

Fig. 4 Frequency distribution of the variation in favourabilities within genetic conservation units with more than one target tree species.

climate change than units in rather flat countries (e.g., Finland, Latvia, Lithuania or Poland).

Comparisons of all 86 tree species show again that species in the units of mountainous habitats (e.g., silver fir, European larch and Swiss stone pine) are less endangered than units with lowland species (Fig. S8b). For the six selected target species, units with pedunculate oak as a target species are expected to experience the fastest changes (on average 1.1 km yr^{-1}), while at units with the closely related sessile oak the velocity of change is only 0.33 km yr^{-1}. The mountainous species silver fir, European beech and Norway spruce are expected to face much lesser velocities of change between 0.15 and 0.22 km yr^{-1} on average (Fig. 3d).

Overall risk assessment

In addition to vulnerability measures for species and units, single units need to be evaluated for focused monitoring and conservation efforts. For an overall risk assessment, we combined the velocity of climate change for a given unit with the favourability of the respective target tree species under current and future climate conditions (Fig. 5). The charts in Fig. 5 also include two critical thresholds of the climate niche models (RS95 and the observed prevalence of the GAM). Conservation units containing target species in the upper-right corner of the graph can be considered as less vulnerable, in particular if they are above a favourability of 0.5 (=the observed prevalence). However, also within the 'lower-risk' category, single units will experience a high velocity of climate change and might therefore require additional conservation measures. Species in conservation units on the lower left side of Fig. 5 are the most susceptible to climate change because they are already at the species climatic distribution limits today and will be far below the species limits in the future.

Correlation analysis between the velocity of climate change, the species' favourabilities and the favourabil-
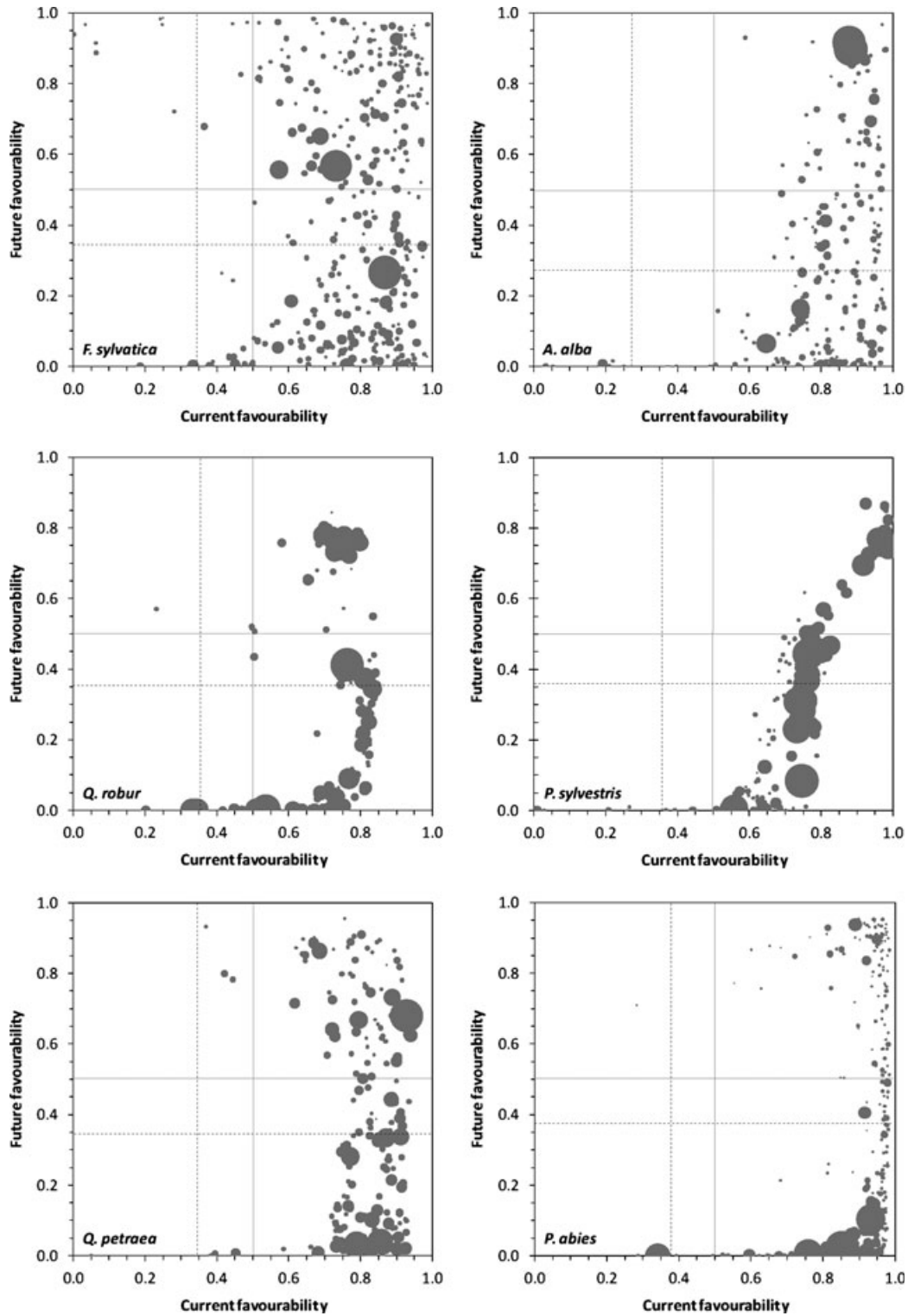
Fig. 5 Vulnerability of six selected target species within the genetic conservation units. The figures relate the current favourability of a unit for the respective species to its favourability in the future. The size of the circle shows the expected velocity of change. Thresholds are given for a required sensitivity of 95% (black dashed lines) and the prevalence observed in the models (grey continuous lines). Populations in the upper-right corner are less endangered because they match the climatic conditions very well, whereas tree populations in the lower left corner are expected to have experienced stressful climatic borders already in the past and might thus contain local adaptations. Tree populations in the left upper border will likely have better conditions in the future than today.

Table 2 Concordance of the calculated climate risk measures for the six analysed target species as tested by correlations between the velocity of climate change within conservation units and the favourabilities (*F*) under current and future conditions as well as the favourability change (Δ*F*).

Species	Velocity vs. F_{curr}	Velocity vs. F_{fut}	Velocity vs. ΔF
A. alba	0.042	0.177*	−0.161*
P. abies	−0.254*	−0.156*	0.076
P. sylvestris	0.227*	0.177*	−0.015
Q. robur	−0.190*	−0.060	−0.001
Q. petraea	0.115	−0.040	0.071
F. sylvatica	0.006	−0.077	0.074

*significant correlations

ity change revealed a low consistence between the different climate risk measures (Table. 2). However, low but significant negative correlations were obtained for Norway spruce and pedunculate oak, suggesting that for these species units with low favourabilities also will experience faster environmental changes. In contrast, significant positive correlations were found for Scots pine and silver fir. The low correlation between the velocity of change and species favourabilities is also evident from the geographic distribution of vulnerabilities as given in Fig. 1d for sessile oak and Fig. S9 for other species.

Discussion

In comparison to the forests of eastern Asia and North America, European forests harbour a lower diversity of tree species mainly due to major climate changes in the Pliocene and the subsequent climatic oscillations during Quaternary (Campbell, 1982). In particular, the loss of habitats with a moist warm-temperate climate in the Mediterranean was found to have caused the extinction of less cold and drought tolerant taxa (Svenning, 2003). The current anthropogenic climate warming is expected to cause similar environmental changes at much shorter time scales, and several studies have already projected the drastic consequences for tree species' distribution ranges and diversity (e.g., Sykes *et al.*, 1996; Thuiller *et al.*, 2006) and evaluated the different climate-related risk factors for various tree species (Ohlemüller *et al.*, 2006). So far, however, few studies addressed the effect of climate change on intraspecific genetic variation and on the manifold local adaptations within the species ranges (but see Hamann & Aitken, 2013).

The vulnerability analysis of the individual genetic conservation units and the network using species-specific niches models revealed a higher risk in units at

the species southern distribution limit. Here, the target species within a majority of conservation units will be located outside or at the extreme border of the species current environmental niches. The risk analysis for the individual species also showed gaps within the current network to cover the full climatic niche of target species under current conditions. In particular, our analyses demonstrated that for three of the six investigated tree species, units at the colder end of the climatic niche are overrepresented while fewer units are currently available at the warm and dry end of its distribution. The advantage of this discrepancy is that species within conservation units are less affected by climate changes than within the species' average habitats. On the other hand, if the present warm end of the species distribution is underrepresented within the network (e.g., for the two oak species and Norway spruce), it is very likely that certain local adaptations are not covered and might be lost in the near future. This is in agreement with an ecological gap analysis of Lefèvre *et al.* (2013), where several species were found to be underrepresented in marginal parts of their distribution. Therefore, genetic conservation should aim to identify and integrate additional populations at the warm and dry end of species niches. Such populations are likely to retain genetic resources of high value also for other areas as it has been shown for example for Norway spruce populations in Austria (Schueler *et al.*, 2013). A contrasting situation was found for Scots pine: its populations at the less-endangered cold border of the niche are underrepresented.

The species-specific risk analysis within the present study focused on six of the economic and ecologically most important tree species in European forests, all of them present within larger numbers of genetic conservation units. In contrast to Mediterranean species, boreal and deciduous species are predicted to suffer mainly from the loss of suitable area (e.g., Ohlemüller *et al.*, 2006) but their disappearance will also result in reduced incomes for forest owners and the timber industry as well as reduced carbon sequestration in European forests (Hanewinkel *et al.*, 2012). In addition, the genetic conservation network covers another 80 species in 1200 units, but many species can be found only within a small number of units. Also, conservation units and the respective native species in Mediterranean forests are so far underrepresented in the network (Lefèvre *et al.*, 2013). Therefore, a species-specific analysis of these species for the network of genetic conservation units is not meaningful. For these species, other nature conservation activities, such as areas documented in the World Database of Protected Areas should be included for several reasons: firstly, to identify populations with potential local adaptations to spe-

cific environmental condition and secondly, to expand genetic conservation activities to the full spectrum of environmental conditions under which the species occurs. The six analysed species were found to be at high risk of local extinction, i.e. below the observed 95% occurrences, in between 33% (European beech) and 65% (Norway spruce) of their current conservation units. Only within a very small number of units, the future conditions will result in higher favourabilities for the respective species. A very similar ratio of conservation areas unsuitable for plant species under future climate conditions was previously found in an analysis of European protected and Natura 2000 areas (Araújo *et al.*, 2011).

Many countries have established units for several co-occurring and ecologically comparable tree species following a site-oriented conservation approach (Lefèvre *et al.*, 2013). By comparing the favourabilities among target species within single units, we found that the variation in favourabilities more than doubled. This suggests that multi-species units might not ensure the long-term conservation of all target species currently present. Conservation management might therefore need to focus on those species that have the highest potential to survive in future climates.

Our more general vulnerability analysis on the basis of the velocity of change showed, in agreement with worldwide studies on ecosystem changes (Loarie *et al.*, 2009), that units within flat and homogeneous terrain and species that rather occur within such habitats will undergo a higher velocity of change than units in mountainous regions. For individual species, these results are partly in contrast to the favourability analysis, according to which the coniferous and mountainous species (e.g., silver fir, Norway spruce) will experience the strongest decrease in favourabilities within the conservation units. Also, the correlation between the change velocity and the species favourabilities is low. This is because the velocity of climate change includes the effect of the topographic complexity, which was found to play an important role in determining vegetation types and the putative occurrence of microrefugia (Dobrowski, 2011; Lenoir *et al.*, 2013). So far, we cannot state for each individual unit whether its topography is sufficiently complex or not to enable the survival of target species also under future conditions. However, the results suggest that monitoring and management activities should consider more topographic structure and take into account local landscape characteristics in conservation decisions. Velocity measures are also important for the revision of national conservation strategies because the high velocity within some countries and the strong variation among countries is likely to create problems for the implementation of these strategies,

particularly in smaller countries. Both indices of vulnerability will be made available through the database www.eufgis.org and communicated to the national focal points. Practitioners might interpret the favourability values F according to the species thresholds. Here, $F > OP_F$ can be considered to be at low risk, $OP_F > F > RS95_F$ are at medium risk and $F < RS95_F$ are at high risk. Also, the specific location and size of units within the plots of present and future favourabilities (Fig. 5) provide a valuable assessment of its vulnerability status. Immediate monitoring and conservation efforts should be given in particular to conservation units below $RS95_F$, in particular if they also experience a large velocity of change (=circles with a large area). Trees within units at the lower left side of the graph have already experienced harsh climate conditions in the past and might thus be candidates to identify local adaptations to future climates.

Genetic conservation in the present network considerably differs from other conservation efforts: while in many other conservation areas management is restricted, the concept of the dynamic conservation of genetic resources allows and promotes active management to maintain the genetic processes (i.e. gene flow, pollination, regeneration) of the target species (Koskela *et al.*, 2013). The management of the conservation units may also include common silvicultural measures and even artificial regeneration is allowed as long as the reproductive material originates from the same unit. These activities help to ensure the long-term persistence of conserved tree populations also under climate change because biotic interactions such as forest pests or competing trees can be reduced to a minimum. Such interactions were found to be serious limits for realized species niches (Meier *et al.*, 2011; Hellmann *et al.*, 2012). Consequently, the present risk analysis only provides a proxy for the vulnerability of conservation units and species within units rather than an absolute measure of threat.

Another methodological limitation of the present study is the applied climate niche model. Within the recent decade, species distribution models on basis of species climatic niches have become a widely used tool to understand species' climatic and migrational limitations (Svenning & Skov, 2004; Randin *et al.*, 2013), to forecast its future distribution ranges (Sykes *et al.*, 1996), or to analyse the impact of climate change on biodiversity (Thomas *et al.*, 2004; Thuiller *et al.*, 2011), ecosystem functions (Hanewinkel *et al.*, 2012) and conservation activities (Araújo *et al.*, 2011; Summers *et al.*, 2012). However, although manifold statistical modelling techniques are available, the integration of genetic variation within species and the species adaptive potential and plasticity into niche models is still a

challenging task (Harte *et al.*, 2004; McMahon *et al.*, 2011) that would strongly increase the reliability of model projections. For example, Oney *et al.* (2013) applied universal transfer functions (O'Neill *et al.*, 2008) on the basis of provenance test data to model species distribution under current and future climates. Their model was found to produce statistically improved projections and a less stringent species distribution than the classical model. Also, standard species distributions models, based on presence–absence data applied for different phylogeographic lineages or subspecies, were found to perform better than models that treat species as single entities (Pearman *et al.*, 2010; D'Amen *et al.*, 2012; Oney *et al.*, 2013). Although such model approaches would be valuable also for the target species of the present study, it would not allow an unbiased comparison of climate threats among conservation units. Therefore, we decided to use an independent dataset of presence–absence data and to build general climate niche models for each target species in order to allow a relative comparison of climate risks among units. We decided to focus on GAMs as a single modelling approach and carried out a careful data calibration because single models on the basis of improved data and careful cross-validation might result in equal or even better forecasts than consensus model predictions (Marmion *et al.*, 2009). Optimized GAMs were found to be well suited also if extrapolated beyond the range of the initial data (Fensterer, 2010; Mellert *et al.*, 2011). In order to describe the potential distribution, a high sensitivity of 95% was defined as risk level and model probabilities were transformed into favourabilities to allow a comparison among species. Overall, this approach is well suited for the unbiased comparison among species and conservation units in the present study because it better reflects the ecological potential of the species than their realized niches. Such fundamental niche models already cover a variety of extrinsic (e.g., forest pests) and intrinsic factors (e.g., plasticity), given that these factors have shaped the occurrence of tree species in the Level-I plots (ICP Forests, 2010). In addition, climate-independent factors are also expected to affect tree health and to contribute to the persistence of specific populations. For example, Namkoong *et al.* (1996) proposed several genetic indicators as demographic and genetic verifiers for population vulnerability and sustainability. Given that sufficient demographic and genetic data are available for certain populations, e.g., within genetic monitoring programmes (Konnert *et al.*, 2011), these indictors might be used to estimate also intrinsic, population-specific vulnerabilities. So far, however, only incomplete demographic and no genetic data are available for the units of genetic conservation network, and thus

exact estimates of population vulnerabilities cannot be estimated (Lefèvre *et al.*, 2013).

Besides the calculated risk factors for specific units and target species and the identified gaps in the conservation network, the present study shows a need for intensified monitoring and continued conservation measures. The differences in average vulnerabilities among the individual countries indicate that conservation of forest genetic resources should be planned and coordinated at the pan-European level. In particular, the following lessons should be considered by future conservation programmes:

1. Intensified monitoring in high risk conservation units: for practical management (and scientific analysis) of populations at the species climatic borders more intensive monitoring is strongly needed. Such monitoring will also aid to improve our scientific understanding of selective processes within stressful environments and may result in the utilization of existing or upcoming local adaptations. However, this suggestion is in contrast to actual proposals on the financial focusing of conservation measures to climatic stable conservation areas (Iwamura *et al.*, 2010). For genetic conservation of trees such prioritizing of conservation investments would certainly lead to an unrecoverable loss of locally adapted genotypes which are necessary for the long-term survival of the species.
2. Populations within high risk units should be considered for complementary conservation measures, i.e. the establishment of dynamic *ex situ* conservation units within regions with lower risk or the creation of static *ex situ* collections. Most notably, assisted migration, i.e. the facilitated movement of populations to track the movement of the climate to which they are adapted to, should be considered as part of adaptation and conservation strategies (Leech *et al.*, 2011). The main requisite for these activities is increasing co-operation at the transnational level: so far daily monitoring and management actions on genetic resources are mainly implemented on the national level. Activities on transnational level, however, require sustainable coordination and funding opportunities on the European level.
3. Increase the size of conservation units: this could by a very simple but useful management action, mainly if conservation units are located in mountainous terrains. If possible, such an increase will substantially reduce the velocity of change experienced by the respective target species. So far, the size of many units is rather small: about two-third

of the existing conservation units are smaller than 100 ha (Lefèvre *et al.*, 2013).

4. Complementation of the current network with populations at range margins in particular at the warm end of the species climate niches. Additional units might also include other protected areas (e.g., biodiversity conservation), if they fulfil the minimum requirements for genetic conservation units and if they add additional local adaptations.

Acknowledgement

References

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climatic changes outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

Alberto FJ, Aitken SN, Alìa S *et al.* (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.

Araújo MB, Alagador D, Cabeza M, Nogués-Bravo D, Thuiller W (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.

Bohn U, Neuhäusl R (2003) Map of the natural vegetation of Europe. Scale 1: 2 500 000. Landwirtschaftsverlag, Münster, Germany.

Buschbom J, Yanbaev Y, Degen B (2011) Efficient long-distance gene flow into an isolated relict oak stand. *Journal of Heredity*, **102**, 464–472.

Campbell JJN (1982) Pears and persimmons: a comparison of temperate forests in Europe and eastern North America. *Vegetatio*, **49**, 85–101.

Connolley WM, Bracegirdle TJ (2007) An Antarctic assessment of IPCC AR4 coupled models. *Geophysical Research Letters*, **34**, L22505.

D'Amen M, Zimmermann NE, Pearman PB (2012) Conservation of phylogeographic lineages under climate change. *Global Ecology and Biogeography*, **22**, 93–104.

Dobrowski SZ (2011) A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, **17**, 1022–1035.

Eriksson G, Namkoong G, Roberds JH (1993) Dynamic gene conservation for uncertain futures. *Forest Ecology and Management*, **62**, 15–37.

Estrada A, Real R, Vargas JM (2008) Using crisp and fuzzy modelling to identify favourability hotspots useful to perform gap analysis. *Biodiversity and Conservation*, **17**, 857–871.

Falk W, Mellert KH (2011) Species distribution models as a tool for forest management planning under climate change: risk evaluation of *Abies alba* in Bavaria. *Journal of Vegetation Science*, **22**, 621–634.

Fensterer V (2010) Statistical methods in niche modelling for spatial prediction of forest tree species. Diploma thesis, University Munich. Available at http://epub.ub.uni-muenchen.de/11579/

Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38–49.

Freeman EA, Moisen G (2008) PresenceAbsence: An R Package for Presence-Absence Model Analysis. *Journal of Statistical Software*, **23**, 1–31.

Game ET, Lipsett-Moore G, Saxon E, Peterson N, Sheppard S (2011) Incorporating climate change adaptation into national conservation assessments. *Global Change Biology*, **17**, 3150–3160.

Gavin DG, Hu FS (2006) Spatial variation of climatic and non-climatic controls on species distribution: the range limit of *Tsuga heterophylla*. *Journal of Biogeography*, **33**, 1384–1396.

Hamann A, Aitken SN (2013) Conservation planning under climate change: accounting for adaptive potential and migration capacity in species distribution models. *Diversity and Distributions*, **19**, 268–280.

Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Hamrick JL, Godt MJW (1996) Effects of Life History Traits on Genetic Diversity in Plant Species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **351**, 1291–1298.

Hamrick JL, Godt MJW, Sherman-Broyles SL (1992) Factors influencing levels of genetic diversity in woody plant species. *New Forests*, **6**, 95–124.

Hanewinkel M, Cullmann DA, Schelhaas MJ, Nabuurs G-J, Zimmermann NE (2012) Climate change may cause severe loss in the economic value of European forest land. *Nature Climate Change*, **3**, 203–207.

Hannah L (2010) A global conservation system for climate-change adaptation. *Conservation Biology*, **24**, 70–77.

Hannerz M, Sonesson J, Ekberg I (1999) Genetic correlations between growth and growth rhythm observed in a short-term test and performance in long-term field trials of Norway spruce. *Canadian Journal of Forest Research*, **29**, 768–778.

Harte J, Ostling A, Green JL, Kinzig A (2004) Climate change and extinction risk. *Nature*, **430**, 33.

Hastie TJ, Tibshirani RJ (1990) *Generalized additive models*. Chapman & Hall, London, UK.

Hellmann JJ, Prior KM, Pelini SL (2012) The influence of species interactions on geographic range change under climate change. *Annals of the New York Academy of Sciences*, **1249**, 18–28.

Higgins SI, O'Hara RB, Römermann C (2012) A niche for biology in species distribution models. *Journal of Biogeography*, **39**, 2091–2095.

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hirzel AH, Le Lay G (2008) Habitat suitability modelling and niche theory. *Journal of Applied Ecology*, **45**, 1372–1381.

Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences USA*, **106**, 19659–19665.

Hurme P, Repo T, Savolainen O, Pääkkönen T (1997) Climatic adaptation of bud set and frost hardiness in Scots pine (*Pinus sylvestris*). *Canadian Journal of Forest Research*, **27**, 716–723.

Hutchinson MF (1957) Concluding remarks. In *Cold Spring Harbour Symposia on Quantitative Biology, population studies: animal ecology and demography*, vol. **22**, Cold Spring Harbor, New York, 415–427.

ICP Forests, 2010: *Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests*. UNECE ICP Forests Programme Co-ordinating Centre, Hamburg [http://www.icp-forests.org/Manual.htm] (accessed 11 October 2012).

Iwamura T, Wilson KA, Venter O, Possingham HP (2010) A climatic stability approach to prioritizing global conservation investments. *PLoS ONE*, **5**, e15103.

Jump AS, Mátyás C, Peñuelas J (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, **24**, 694–701.

Konnert M, Maurer W, Degen B, Kätzel R (2011) Genetic monitoring in forests - early warning and controlling system for ecosystemic changes. *iForest*, **4**, 77–81.

Koskela J, Lefèvre F, Schueler S *et al.* (2013) Translating conservation genetics into management: Pan-European minimum requirements for dynamic conservation units of forest tree genetic diversity. *Biological Conservation*, **157**, 39–49.

Kremer A, Ronce O, Robledo-Arnuncio JJ *et al.* (2012) Long distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, **15**, 378–392.

Kuparinen A, Savolainen O, Schurr FM (2010) Increased mortality can promote evolutionary adaptation of forest trees to climate change. *Forest Ecology and Management*, **259**, 1003–1008.

Ledig FT (1986) Conservation strategies for forest gene resources. *Forest Ecology and Management*, **14**, 77–90.

Leech SM, Lara Almuedo PL, O'Neill G (2011) Assisted Migration: adapting forest management to a changing climate. *BC Journal of Ecosystems and Management*, **12**, 18–34.

Lefèvre F, Koskela J, Hubert J *et al.* (2013) Dynamic Conservation of Forest Genetic Resources in 33 European Countries. *Conservation Biology*, **27**, 373–384.

Lenoir J, Graae BJ, Aarrestad PA *et al.* (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, **19**, 1470–1481.

Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature*, **462**, 1052–1055.

Marmion M, Parviainen M, Luoto M, Heikkinen RK, Thuiller W (2009) Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, **15**, 59–69.

McMahon SM, Harrison SP, Armbruster WS *et al.* (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution*, **26**, 249–259.

Meier ES, Edwards TC Jr, Kienast F, Dobbertin M, Zimmermann NE (2011) Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica*. *Journal of Biogeography*, **38**, 371–382.

Mellert KH, Fensterer V, Küchenhoff H, Reger B, Kölling C, Klemmt HJ, Ewald J (2011) Hypothesis-driven species distribution models for tree species in the Bavarian Alps. *Journal of Vegetation Science*, **22**, 635–646.

Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology*, **96**, 784–794.

Namkoong G (1997) A gene conservation plan for loblolly pine. *Canadian Journal Forest Research*, **27**, 433–437.

Namkoong G, Boyle T, Gregorius H-R, Joly H, Savolainen O, Wickneswari R, Young A (1996) Testing Criteria and Indicators for Assessing the Sustainability of Forest Management: Genetic Criteria and Indicators. Working Paper No. 10, Center for International Forestry Research, Bogor.

Nathan R, Horvitz N, He Y, Kuparinen A, Schurr FM, Katul GG (2011) Spread of North American wind-dispersed trees in future environments. *Ecology Letters*, **14**, 211–219.

Ohlemüller R, Gritti ES, Sykes MT, Thomas CD (2006) Quantifying components of risk for European woody species under climate change. *Global Change Biology*, **12**, 1788–1799.

O'Neill G, Hamann A, Wang T (2008) Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.

Oney B, Reineking B, O'Neill G, Kreyling J (2013) Intraspecific variation buffers projected climate change impacts on *Pinus contorta*. *Ecology and Evolution*, **3**, 437–449.

Pan Y, Birdsey RA, Fang J (2011) A large and persistent carbon sink in the world's forests. *Science*, **333**, 988–993.

Pearman PB, D'Amen M, Graham C, Thuiller W, Zimmermann N (2010) Within-taxon niche structure: niche conservatism, divergence and predicted effects of climate change. *Ecography*, **33**, 990–1003.

Randin CF, Paulsen J, Vitasse Y, Kollas K, Wohlgemuth T, Zimmermann NE, Körner C (2013) Do elevational limits of deciduous tree species match with their thermal latitudinal limits? *Global Ecology and Biogeography*, **22**, 913–923.

Real R, Barbosa AM, Vargas JM (2006) Obtaining environmental favourability functions from logistic regression. *Environmental and Ecological Statistics*, **13**, 237–245.

Rehfeldt GE, Tchebakova NM, Parfenova YI, Wykoff WR, Kuzmina NA, Milyutin LI (2002) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology*, **8**, 912–929.

Robledo-Arnuncio JJ (2011) Wind pollination over mesoscale distances: an investigation with Scots pine. *New Phytologist*, **190**, 222–233.

Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 595–619.

Schueler S, Schlünzen KH (2006) Modelling of oak pollen dispersal on the landscape level with a mesoscale atmospherical model. *Environmental Modeling and Assessment*, **11**, 179–194.

Schueler S, Kapeller S, Konrad H *et al.* (2013) Adaptive genetic diversity of trees for forest conservation in a future climate: a case study on Norway spruce in Austria. *Biodiversity and Conservation*, **22**, 1151–1166.

St. Clair BJ, Howe GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biology*, **13**, 1441–1454.

Summers DM, Bryan BA, Crossman ND, Meyer WS (2012) Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. *Global Change Biology*, **18**, 1365–2486.

Svenning J-C (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. *Ecology Letters*, **6**, 646–653.

Svenning J-C, Skov F (2004) Limited filling of potential range in European tree species. *Ecology Letters*, **7**, 565–573.

Sykes MT, Prentice IC, Cramer W (1996) A Bioclimatic Model for the Potential Distributions of North European Tree Species Under Present and Future Climates. *Journal of Biogeography*, **23**, 203–233.

Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.

Thuiller W, Lavorel S, Sykes MT, Araújo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions*, **12**, 49–60.

Thuiller W, Lavergne S, Roquet C, Boulangeat I, Lafourcade B, Araujo MB (2011) Consequences of climate change on the tree of life in Europe. *Nature*, **470**, 531–534.

Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wood SN (2006) *Generalized additive models – an introduction with R*. Chapman & Hall, Boca Raton, FL, US.

Wood SN (2009) mgcv: GAMs with GCV/AIC/REML smoothness estimation and GAMMs by PQL. R package ver. 1.6-1. Available at: http://cran.r-project.org/web/packages/mgcv/index.html (accessed 20 February 2013)

Woodward FI (1990) The impact of low-temperatures in controlling the geographical-distribution of plants. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **326**, 585–593.

Zarnetske PL, Edwards TC, Moisen GG (2007) Habitat classification modeling with incomplete data: Pushing the habitat envelope. *Ecological Applications*, **17**, 1714–1726.

Supporting Information

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

Figure S1. Impact of the individual climate parameters on the proportion of explained deviance (ΔDev rel) of the generalized additive models of the species' environmental niche for single target species.

Figure S2. Response functions of the individual climate parameters within the generalized additive models of the species' environmental niche for single target species.

Figure S3. Results of the tenfold cross-validation of species distribution models given as *AUC*. Boxes mark the 25–75% quartile, whiskers the 1.5 interquartile range and the solid line the median of the ten cross-validation runs.

Figure S4. Present and future distribution of selected target tree species as revealed from species distribution model and the representation of species within the network of genetic conservation units.

Figure S5. Present and future distribution of selected target tree species as revealed from species distribution model and the representation of species within the network of genetic conservation units.

Figure S6. Share of genetic conservation units (GCUs) which show lower (Loser) or higher (Winner) favourabilities under climate conditions of 2100.

Figure S7. Changing environmental conditions for the European network of genetic conservation units (black dots): (a) Temperature increase between current and future conditions for Europe, (b)velocity of climate change following Loarie *et al.* (2009).

Figure S8. Velocity of climate change given as average value for the genetic conservation units per (a) country and per (b) target tree species.

Figure S9. Natural distribution of the six analysed target species according to EUFORGEN distribution maps and the climate risks within the individual GCUs according to two calculated risk indices. The favourabilities F within units is shown according to the threshold of modelled climate niche. Green: $F > 0.5$ (=observed prevalence); Yellow: $0.5 > F > RS95$; Red: $F < RS95$. The velocity of change is indicated by the size of the dots (larger dots = higher velocity).