



Realized and potential climate niches: a comparison of four *Rhododendron* tree species

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Abstract

Aim This study aims to evaluate the hypothesis that there is no difference between the realized and the *ex-situ* niches of four selected *Rhododendron* tree species. If the hypothesis is rejected, the aim is: (1) to evaluate whether the magnitude of discrepancy between the two types of niche is related to competition or external constraint, and (2) to identify which niche dimension is expanded (cold and/or warm limits) and to discuss it in relation to the assumption behind the biogeographical projections related to global warming.

Location The four target species (*Rhododendron arboreum* Sm., *R. campanulatum* D. Don, *R. barbatum* Wall., and *R. wallichii* Sm.) are common evergreen broad-leaved trees in the central Himalayas. Their realized niches are based on data from the elevation-temperature gradient in Nepal (1000–5000 m a.s.l.). The *ex-situ* data are from botanical gardens and arboreta mainly located in the northern hemisphere ($n = 43$).

Methods Binary data on these taxa were obtained from 707 geocoded herbarium specimens (elevation and UTM location) and from two elevation transects in Nepal ($n = 194$ plots). Climate conditions from *ex-situ* locations for each taxon were compared with their realized climate ranges with respect to (i) mean annual temperature (MAT), (ii) mean minimum temperature of the coldest month (MINCM), (iii) mean maximum temperature of the warmest month (MAXWM), and (iv) moisture index (MI). Realized optima were estimated by Generalized Linear Models (GLM), and its non-parametric extension, Generalized Additive Models (GAM), were used to estimate the realized niches.

Results All target species have *ex-situ* individuals outside the realized climate niche, but the number is much higher for maximum and minimum variables than for MAT. The most dominant species (*in-situ*), *R. arboreum*, had very few individuals outside its realized range, indicating congruence between its *ex-situ* and realized niches. The other taxa had many individuals outside the warm end of their realized temperature ranges, but almost none beyond the cold end of their ranges. All target taxa occur in common gardens under warm temperate conditions, but only *R. arboreum* grows in the warm temperate zone in the Himalayas. This trend at the warm end of the gradient is interpreted as a result of biotic exclusion.

Main conclusion The results demonstrate that an extreme cold temperature may represent an absolute boundary for tree species' survival, whereas warm temperatures do not. This is in agreement with the hypothesis that several tree species may survive global warming *in-situ* because of high temperature tolerance, but its effect on regeneration is uncertain. In lieu of this there may be a significant time lag between change in climate and transient tree species distribution. Thus the effect of global warming on tree species distribution may be very difficult to predict.

Keywords

Arboreta, climate warming, elevation gradient, the Himalayas, response surface.

INTRODUCTION

Climate is considered to be a primary determinant in the distribution of plant species (Woodward, 1996; Cox and Moore, 2000). Attempts to predict plant responses to future climatic change depend on knowledge of individual species responses to present temperature and rainfall (Austin, 1992). Several studies have used estimated realized climate niches to predict potential biogeographical changes in species distribution (e.g. Flannigan & Woodward, 1994; Huntley *et al.*, 1995; Sykes *et al.*, 1996; Shugart, 1998). These projections assume that (i) species have a simple gaussian response function with an optimum in the middle of the estimated climate range for a given climate variable, (ii) species are (or were) in equilibrium with the macroclimate, and (iii) negative interaction between species is redundant for biogeographical patterns, i.e. that the realized niche is a good approximation of the fundamental niche.

The rationale underlying these assumptions has been criticized: (i) Austin (1982, 1992) argues that the optimum of the realized niche may differ significantly from the fundamental niche, and the response is not necessarily symmetric around the range centre, (ii) Hengeveld (1997) has pointed out that a good correlation between climate and species distribution does not imply that species are in equilibrium with the macroclimate, and (iii) Schrenk (1996) and Loehle & LeBlanc (1996) point to the well-known fact that climate is not the only factor that determines the geographical distribution of trees. Although all organisms are influenced by climate, the changes in actual geographical distribution will depend on all kinds of biotic factors such as competition, dispersal and pathogens, i.e. biotic exclusion. Thus it is only the theoretical fundamental climate niche (i.e. without biotic interactions) that will change its geographical distribution in direct response to a change in climate.

There are few studies that experimentally demonstrate the difference between the fundamental and the realized niches, but some important contributions have been made by Ellenberg (1953), Mueller-Dombois & Ellenberg (1974), Ernst (1978); and Austin with co-workers (Austin & Austin, 1980; Austin, 1982; Austin *et al.*, 1985; see also Davis *et al.*, 1998 for zoological example). However, forest nurseries and arboreta have demonstrated that some trees are capable of growing outside the climate niche where they grow naturally (e.g. Hellmers & Rook, 1973; Wright, 1976; Korzukhin *et al.*, 1989; Booth, 1996). Loehle & Le Blanc (1996) state that several projections of biogeographical changes in tree species distribution fail to take into consideration that species may survive under the new climate regime. One may view planting of trees in arboreta as a long-term experiment (*sensu lato*), thus a compilation of such data can be used to

evaluate the potential differences between the realized and the *ex-situ* niche. The survival in *ex-situ* conditions can be interpreted as a proxy of the fundamental niches as the biotic interaction is reduced. However, *ex-situ* survival will not indicate whether the tree species will survive over generations as the regeneration phase is artificially facilitated. The term potential climate niche is used for the *ex-situ* survivals. A systematic comparison between the realized climate niche and climate at the *ex-situ* sites is a novel approach, but a few such analyses have been made on *Eucalyptus* (Booth, 1996) (see also Jäger, 1975/76).

This study investigates whether four selected *Rhododendron* species are able to survive outside their realized climate niches. The realized niche is based on data from one of the longest elevation-temperature gradients in the world, i.e. the Himalayan elevation gradient, whereas the *ex-situ* data come from botanical gardens and arboreta. The realized niche is partly limited by negative interaction from other species, especially between species with similar growth form. As the target rhododendrons have the same growth form (small evergreen trees) and are closely related taxonomically (all can hybridize) (Chamberlain, 1982), there is good reason to assume that interspecific competition is present. One may also hypothesize that dominant species (assumed successful competitors) have less discrepancy between the two types of niche than more infrequent subordinate species. This hypothesis is congruent with the idea that dominant species are regularly distributed along a gradient (assumed effect of resource partitioning), whereas subordinate species are more irregularly distributed (Gauch and Whittaker, 1972).

The primary aim is to test the hypothesis that there is no difference between the realized and the *ex-situ* potential niches. If this hypothesis is rejected, the secondary aims are (1) to evaluate if the magnitude of discrepancy between the two types of niche is related to competition or external constraint, and (2) to identify which niche dimension is expanded (cold and/or warm limits). The results will also be discussed in relation to the assumption behind the biogeographical global warming projections.

MATERIALS AND METHODS

Species and data sources

The four target species (*Rhododendron arboreum* Sm., *R. campanulatum* D. Don, *R. barbatum* Wall. and *R. wallichii* Sm.) are evergreen broad-leaved trees and belong to the subgenus *Hymenanthes* (Chamberlain, 1982). *Rhododendron arboreum* is dominant, whereas the others are subordinate, but *R. campanulatum* may be locally abundant and form sub-alpine forest. Two alpine shrubs (*R. lepidotum* Wall. and *R. anthopogon* D. Don) were

included in the data collection both from herbaria and arboreta (cf. below), but they are not part of the niche comparison. This was carried out to ensure that the analysed temperature gradient goes beyond the presence of the four target species at the cold end of the gradient (cf. Austin *et al.*, 1994; Franklin, 1998). However, there are no *Rhododendron* species occurring at temperatures warmer than those of *R. arboreum*, thus this species was not analysed as binary data, but as frequency (cf. below). The rationale for this is explained in Vetaas (2000a). All *Rhododendron* species included are very common in the central Himalayas, Nepal (Polunin and Stainton, 1986), and together cover an elevation gradient from 1000 to 5000 m a.s.l.

The data sources for the realized niches were (1) herbarium specimens collected in Nepal and (2) field sampling: (i) The herbarium specimens were obtained from four herbaria (Tokyo Institute; Godawri Botanic Garden, Kathmandu; Natural History Museum London, and Royal Botanic Garden, Edinburgh). A total of 707 herbarium specimens with elevation and UTM-location were used. (ii) Binary data on the four target species were also obtained from two elevation gradients in Nepal (Vetaas, 2000a) ($n = 194$ plots). Data on *ex-situ* climate conditions were obtained from forty-three botanical gardens/arboreta, which grew at least one of the six rhododendrons, including the two alpine shrubs (cf. above). These gardens represent forty-three positive replies out of *c.* 300 questionnaires sent out to Arboreta and rhododendron societies (www.uib.no/people/nboov/#QUESTIONNAIRE). The geographical distribution of these forty-three gardens is shown in Appendix 1.

Climate variables

The climate data obtained from the arboreta were mean annual rainfall, mean annual temperature (MAT), mean minimum temperature in the coldest month (MINCM), and mean maximum temperature in the warmest month (MAXWM). The minimum and maximum temperatures were often given as whole integers, thus all values were rounded to whole integers. When these values were not given, the values were obtained from the World climate-mapping programme (Booth, 1990). This was possible because several of the arboreta are located close to large cities (cf. Appendix 1).

The elevation noted for each herbarium specimen was used to estimate MAT for each occurrence, based on a lapse rate of 0.51 °C/100 m in Nepal (Anonymous, 1998; cf. Dobremez, 1976). The MINCM (January in the Himalayas) and the MAXWM (July) were also estimated based on a lapse rate of 0.37 °C/100 m and 0.55 °C/100 m, respectively (Anonymous, 1998). The UTM location for each specimen was superimposed on an iso-rainfall map (mean annual precipitation) produced by the International Centre for Integrated Mountain Development (ICIMOD) (Kathmandu) based on data from HMG Department of Hydrology and Meteorology, Nepal. The isolines are separated by 200 mm intervals, except for intervals higher than 2000 mm, which are separated by 500 mm. A preliminary analysis showed

that mean annual precipitation and temperature at the UTM locations are not correlated. However, the moisture available to plants will be determined by the evapotranspiration rate, which is dependent on the temperature. Thus, a crude moisture index (MI) was produced based on the formula of Holdrige *et al.* (1971) [$MI = \text{mean annual bio-temperature (i.e. temperature } > 0 \text{ } ^\circ\text{C}) \times 58.93 / \text{mean annual precipitation}$]. For simplicity the index was inverted, where values < 1 indicate a negative water balance, and values > 1 indicate a positive water balance. MI is a continuous variable, which is an advantage compared with the precipitation intervals. Another advantage is that, e.g. 2000 mm precipitation at 1500 m a.s.l. has a different value from 2000 mm at 3000 m a.s.l., which is ecologically sound.

Niche comparison

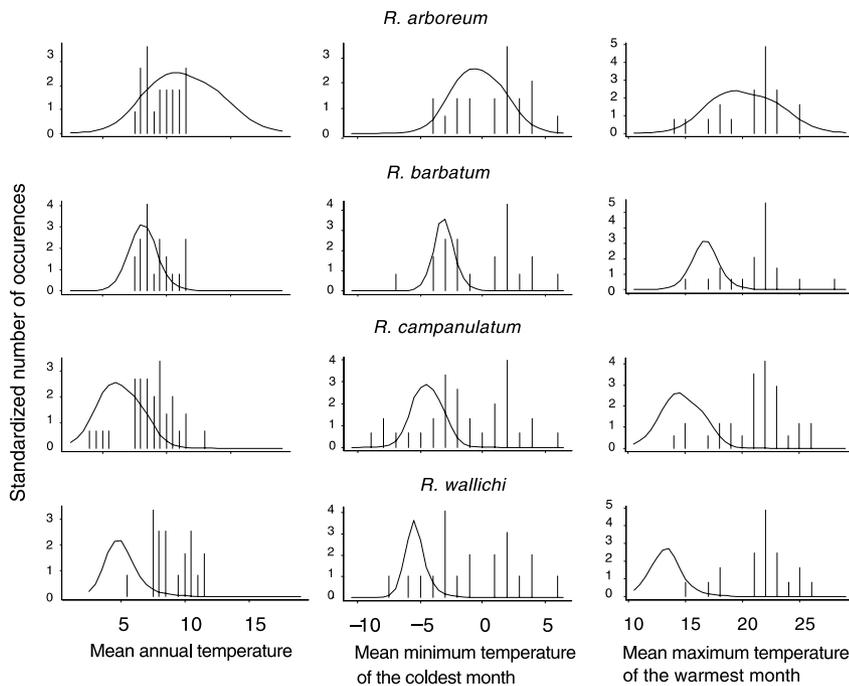
The quality of the data for the realized niche is much better than for the potential niche. The former is based on many herbaria collections and direct field analyses (total $n = 901$), whereas the latter is based on forty-three replies from botanical gardens that have at least one of the target rhododendrons. The garden data are not complete, and have spatial bias with many locations in northern Europe and very few in temperate climates in central and eastern Asia. Thus estimated probability of occurrence does not have the same ecological meaning for the potential niche as for the realized niche. Therefore the evaluation was made by estimating the realized niche and relating this to the *ex-situ* data in three different ways: (i) The realized range was compared with the potential range based on minimum and maximum values documented *in-situ* and *ex-situ* for each variable and species (Table 1). Here the realized optima (Table 1) were estimated by Generalized Linear Models (GLM, Nelder and Wedderburn, 1972) with a logit link function on binomial data (see below) (cf. Yee and Mitchell, 1991; Vetaas, 2000a), whereas the mode was used to indicate the optima of the temperature variables for the *ex-situ* range (Table 1). (ii) The realized range was used to find how many *ex-situ* locations are outside this range, and which side of the realized ranges they are beyond (Table 2). (iii) The realized niches were statistically estimated by Generalized Additive Models (GAM, Hastie and Tibshirani, 1990) and *ex-situ* locations are superimposed on the graphical model (Figs 1 and 2). This was performed to graphically describe the realized niche for each of the species with respect to the different temperature variables. The response variable was the number of occurrences in each 0.5 °C temperature interval. This was divided by standard deviation to accommodate a graphical comparison with the *ex-situ* location, which was superimposed on the niche model with the same standardization (Fig. 1). GAM was also used on binomial data to estimate a two-dimensional realized niche based on MAXWM and MINCM variables, and the climate of the *ex-situ* locations was superimposed on the model (Fig. 2). The two extreme variables, i.e. MAXWM and MINCM, are highly correlated, and thus the graphical niche model primarily show the discrepancy between the

Table 1 Climatic ranges for four *Rhododendron* species in *ex-situ* (ex) and *in-situ* (in) conditions, with respect to mean annual temperature (MAT), mean minimum temperature of coldest month (MINCM), mean maximum temperature of warmest month (MAXWM), and moisture index (MOISTURE)

Variables		<i>R. arboreum</i>		<i>R. barbatum</i>		<i>R. campanulatum</i>		<i>R. wallichii</i>	
		<i>in</i>	<i>ex</i>	<i>in</i>	<i>ex</i>	<i>in</i>	<i>ex</i>	<i>in</i>	<i>ex</i>
MAT	Min	4.4	7.8	6.0	7.7	3.3	4.3	3.5	5.8
	Optimum	11.7	8.8	8.6	8.8	9.8	8.1	4.7	7.8
	Max	19.3	11.6	11.9	11.6	10.2	11.6	10.4	11.6
MINCM	Min	-5.7	-4	-4.6	-7	-6.5	-9	-6.4	-8
	Optimum	-0.7	2	-2.7	2	-4.4	2	-5.5	-3
	Max	5.1	6	-0.3	6	-1.5	6	-1.4	6
MAXWM	Min	12.2	14	13.9	15	11.0	14	11.2	15
	Optimum	19.7	22	16.7	22	14.1	22	12.5	22
	Max	28.2	25	20.3	28	18.4	28	18.7	26
MOISTURE	Min	1.0	0.7	1.5	0.7	1.6	0.7	2.9	0.7
	Optimum	1.8	3.1	4.7	2.2	6.6	1.8	7.5	1.5
	Max	9.6	5.6	6.8	5.6	9.6	5.6	12.0	5.6

Table 2 Number of *ex-situ* individuals of four rhododendron species occurring outside their realized niches with respect to mean annual temperature (MAT), mean minimum temperature of coldest month (MINCM), mean maximum temperature of warmest month (MAXWM), moisture index and rainfall (precipitation)

<i>Ex-situ</i> sites		MAT		MINCM		MAXWM		Moisture		Rainfall	
		Cold	Warm	Cold	Warm	Cold	Warm	Dry	Moist	Dry	Moist
<i>Rhododendron</i>											
<i>arboreum</i>	20	0	0	0	1	0	0	2	0	13	0
<i>barbatum</i>	21	0	0	1	11	0	15	14	0	14	1
<i>campanulatum</i>	33	0	9	4	16	0	27	19	0	6	1
<i>wallichii</i>	20	0	6	1	11	0	16	18	0	12	1

**Figure 1** Response curves of the realized niches for *Rhododendron arboreum* Sm., *R. barbatum* Wall., *R. campanulatum* D. Don., and *R. wallichii* Sm. with respect to mean annual temperature (MAT), mean minimum temperature of coldest month and mean maximum temperature of warmest month. The standardized number of *ex-situ* occurrences is superimposed on the graph (vertical lines). The realized response and the number of *ex-situ* locations are both number of occurrences for each 0.5 °C interval divided by the standard deviation for each species. Note the length of the vertical lines is not directly comparable with the realized response curve.

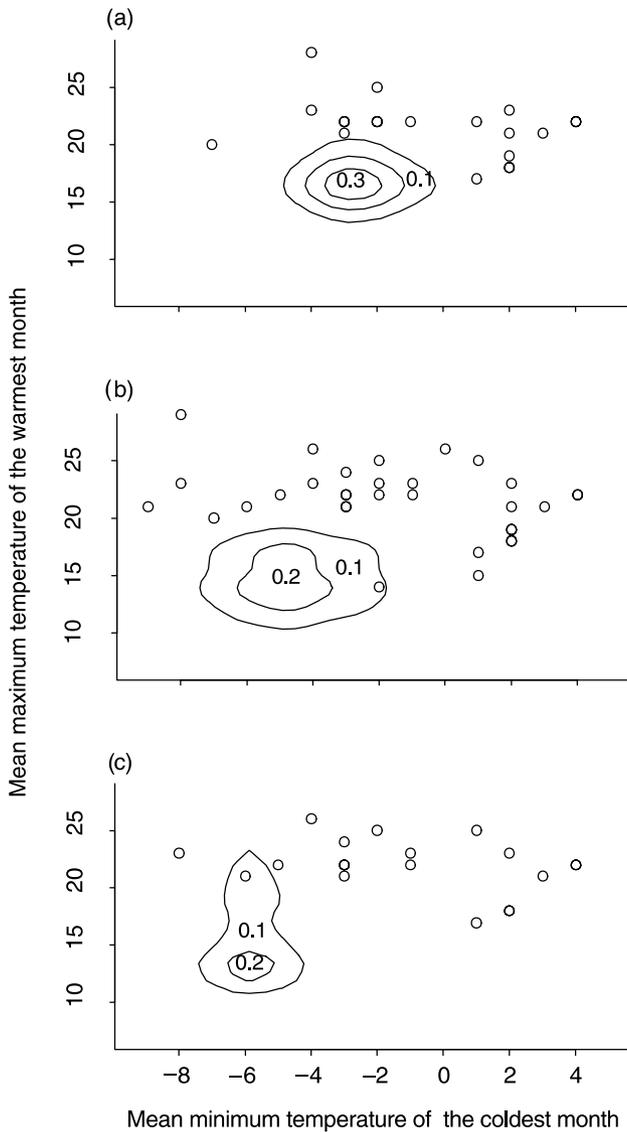


Figure 2 Two-dimensional realized niche defined by mean minimum temperature of the coldest month and mean maximum temperature of the hottest month in the Himalayas. The contours show the probability of occurrence. The data points are *ex-situ* locations of that species, which are superimposed after modelling the realized niche. (a) *Rhododendron barbatum* Wall, (b) *R. campanulatum* D. Don. and (c) *R. wallichii* Sm.

realized niche and the *ex-situ* climate conditions for species with substantial discrepancy. A cubic spline smoother was used in GAM, which allows the data to determine the shape of the response curve instead of being limited by shapes available in parametric regression (i.e. straight lines and parabolas). All analyses were performed using the S-Plus program ver. 4.5 (Anonymous, 1993).

The binomial variable used for the realized niches in Fig. 2 and the realized optima in Table 1 was generated by treating

each taxon as presence (presence of the target *Rhododendron* taxon) and absence (*Rhododendron* taxa other than the target *Rhododendron*) (Vetaas, 2000a). Zero frequencies in Fig. 1 follow the same rationale. This approach relies on the assumption that the number of individuals collected is proportional to the species abundance along the elevation range. The approach proved to be reliable for *R. arboreum*, where response curves based on population density and herbaria data were compared (Vetaas, 2000a).

The idea of constraining the sample location to the occurrence of a genus has been used for environmental niche estimation of *Eucalyptus* species, mainly based on data from *Eucalyptus* forest (Austin *et al.*, 1990), and *Andreaea* mosses (Heegaard, 1997). The rationale for this strategy is that species within a genus have more similar ecology than a random subset of species (i.e. niche conservatism; Prinzing *et al.*, 2001). Thus by restricting the sampling to areas where members of a genus may occur, one avoids inflating the results with an overload of absence values (cf. Austin *et al.*, 1994). The numbers of absence values will be much higher with a more relaxed sampling design in nature (or selection of gardens), but this may not provide more information as potentially they may be far outside the ecological range we are interested in. This applies best to those genera that actually have relatively common ecological requirements, such as the subgenus *Hymenanthes*, but it may not apply to genera that are ecological very heterogeneous. This approach will also implicitly set the limits of the analysed gradient (cf. Austin and Nicholls, 1997), and thus the genus should cover a large part of the target gradient as it does in this study (1000–5000 m a.s.l.).

RESULTS

Realized climate niches

Rhododendron arboreum has the largest temperature range (4.4–19.3 °C) among the target species. *Rhododendron arboreum* hardly overlaps with the other *Rhododendron* species in the interval between optimum and maximum temperatures (Fig. 1, Table 1), except for very minor overlaps with *R. barbatum* (all variables) and *R. campanulatum* (MINCM). The relatively narrow (6 °C) temperature range of *R. barbatum* is within the range of *R. arboreum*, but the optimum is slightly lower than that of *R. arboreum* (Fig. 1, cf. Table 1).

Rhododendron campanulatum has the second largest temperature range, and its optimum is close to the minimum value of *R. arboreum* (Table 1). *Rhododendron wallichii* has a range almost within that of *R. campanulatum*, and its optimum is only slightly colder than that of *R. campanulatum* (Table 1, Fig. 1).

R. campanulatum and *R. wallichii* have the lowest minimum values of the tree-forming rhododendrons, and they may form sub-alpine forest alone or together with *Betula* and *Abies*. *Rhododendron wallichii* differs most from the range of *R. arboreum*, but there is also a large degree of overlap between these two species.

In general, there is a high degree of overlap among the species along the moisture gradient (Table 1). The moisture range of *R. arboreum* is very broad and includes the ranges of almost all other target rhododendrons. The maximum MI for *R. wallichii* reaches 12.0, whereas *R. arboreum* and *R. campanulatum* reach 9.6 (Table 1).

Ex-situ conditions and the realized niche

There are, in general, higher degrees of overlap among *ex-situ* ranges than among the realized ranges, especially for the MI (Fig. 1, Table 1). The *ex-situ* ranges for MAT are in general smaller or of the same magnitude as the realized MAT ranges. The ranges for the other temperature variables are similar or longer than the realized ranges (Table 1). The optima along the two temperature extreme variables (MINCM and MAXWM) are represented by the same mode value for all species, except for *R. wallichii* (MINCM).

Several rhododendrons have survived in *ex-situ* locations with a warmer MAXWM than the respective realized ranges, but only *R. campanulatum* and *R. wallichii* are outside the warm limit of realized MAT range (Table 2). Several of the *ex-situ* locations are located in oceanic climate regimes with warmer MINCM and MAXWM than the rhododendrons experience in the Himalayas. Some arboreta are located in areas with a continental climate with a warmer MAXWM and a colder MINCM than the realized ranges in the Himalayas. Some of these gardens report death because of cold winter temperatures, i.e. below -15°C (Appendix 1).

Only one *ex-situ* individual of *R. arboreum* appears outside the realized temperature niche, and none outside the realized MAT range (Table 2). The MINCM *ex-situ* range is slightly broader than the realized MINCM range, and there are minor differences between the MAXWM ranges.

Several of the *ex-situ* individuals of *R. barbatum* occur in a climate with warmer summer (and winter) temperatures than the realized niche. Thus the *ex-situ* ranges and optima have temperatures higher than the corresponding variables of the realized niches (Fig. 1, Table 2). No *ex-situ* individuals are outside the realized MAT niche, and the realized MAT optimum is only *c.* 0.2°C colder than that of *ex-situ* (Table 1, Fig. 1).

Many *ex-situ* locations of *R. campanulatum* have higher temperatures than the limits of the realized niches (Fig. 1), especially for the MINCM and MAXWM variables (Fig. 2). The *ex-situ* optima for MAXWM and MINCM are outside the realized range, the *ex-situ* range is extended towards warmer temperatures (Tables 1 and 2).

The majority of the *ex-situ* locations for *R. wallichii* are found in a warmer climate than the realized niche (Fig. 1, Table 2). *Rhododendron wallichii* has the biggest difference between the MAT optima (3.1°C) (Table 1). This difference is even greater when MINCM and MAXWM are compared (Fig. 2). The MAXWM optima and MAXWM maxima differ by a magnitude of *c.* $2\text{--}10^{\circ}\text{C}$ between *ex-situ* and *in-situ* conditions (Table 1). The moisture conditions of the

ex-situ locations are all much drier than the natural conditions in the Himalayas (Tables 1 and 2).

DISCUSSION

Dominance and competition

The target species have several *ex-situ* individuals outside their realized climate niches, thus the hypothesis that there is no difference between the realized and the *ex-situ* niches is rejected. However, the discrepancy varies between species and the different climate variables (Table 2). All the rhododendrons seem to survive in a much drier *ex-situ* climate than in the Himalayas, but moisture is easy to manipulate in gardens. Thus actual moisture conditions in gardens are uncertain. It may be inferred that insulating materials can also be used to manipulate temperature, a common practice on frost sensitive species. However, the target species are not regarded as particularly frost sensitive, and it is not common to insulate evergreen species belonging to the Ericaceae family (Brickell, 1992).

It was hypothesized that the dominant species under natural conditions should have less discrepancy between its realized and potential climate niches. This was confirmed by the most dominant species (*R. arboreum*), which had only one individual outside its realized temperature niche. However, the second most dominant species (*R. campanulatum*) had very many. This study did not find *R. arboreum* in *ex-situ* locations outside its realized niche, and may be interpreted as a congruence between its realized and potential climate niches, which is assumed in many of the climate response models (Huntley *et al.*, 1995; Sykes *et al.*, 1996). However, the evidence for congruence between the realized and the potential climate niches would have been stronger if several arboreta had reported failed attempts outside the realized niche. Seven arboreta reported failed attempts, but only three of these are outside the realized range. In all cases the cause of death was not related to the mean variables considered, but to single events of extreme absolute minimum temperatures. However, the probability of a lethal cold temperature is positively correlated to low MINCM temperature close to realized limits.

The congruence between *in-* and *ex-situ* niches of *R. arboreum* may be explained by the fact that *R. arboreum* is a successful competitor that fills its potential niche. This is indicated by its broad temperature range (Table 1, MAT range = 15.0°C), where the coldest half of the range is dominated by ssp. *cinnamomeum* and the warmest by ssp. *arboreum*, with a very narrow overlap around the optimum (Vetaas, 2000b). The splitting into subspecies (Chamberlain, 1982), which grow in different temperature ranges, indicates a high level of genetic variation (Hamrick *et al.*, 1979; Kessel, 1979; Tigerstedt, 1993). This probably has contributed to its dominance in the central Himalayas. Although it is a competitive species, the lack of *ex-situ* individuals beyond the warm limit of the realized range could also be attributed to a lack of suitable soil conditions in warmer climates, which Lenihan (1993) indicated for American tree

species. This applies to all rhododendrons, as they mostly prefer acidic- and humus-rich soil (Cox and Cox, 1997), which is probably uncommon in arboreta located in climates with MAT above 19 °C (i.e. subtropical/tropical climates).

Rhododendron campanulatum provides a biogeographical example of a subdominant taxon, which ranges from subalpine to cold-temperate zones. It is not present in the warm temperate zone in the Himalayas, but survives in a warm temperate climate in arboreta. A majority of its *ex-situ* locations had a climate with summer extremes outside the realized warm limits (Fig. 1). Actually all the target rhododendrons grow together with *R. arboreum* in arboreta in a warm temperate climate (Fig. 1), whereas in central Himalayas *R. arboreum* is the only *Rhododendron* species which grows in the warm temperate zone (Fig. 1) (*R. lepidotum* is occasionally found in disturbed sites). This may indicate that temperature affects the performance of these species in natural conditions and prevents their co-existence, as has been shown for other taxa (Walter and Breckle, 1984; Woodward and Williams, 1987; Flanningan and Woodward, 1994). However, this study cannot indicate whether *R. arboreum* or other biotic factors cause the competitive exclusion.

The realized MAT niche of *R. arboreum* ssp. *cinnamomeum* overlaps with all the other species, but the ssp. *arboreum* is the only dominant *Rhododendron* taxon in the warm temperate zone (Vetaas, 2000b), and the only member of the ericaceous family. A characteristic feature of this zone is that frost events are rare. The MINCM changes from 0.0 °C at 2430 m a.s.l. to -0.3 °C at 2500 m a.s.l., thus on average there will be frost and snow above 2500 m a.s.l. and lack of frost below 2400 m a.s.l. *R. arboreum* ssp. *arboreum* is the only rhododendron taxon that grows where frost is not regular. The change from one single *Rhododendron* taxon to several taxa takes place around 2500 m a.s.l., which coincides with the occurrence of days with frost. If frost is needed to regulate their phenology (cf. below) it will also determine the distribution of these rhododendrons. However, all the target rhododendrons did survive in gardens with a MINCM above 0° (Fig. 1, Tables 1 and 2), which means that they can survive in frost and snow-free locations when biotic exclusion is eliminated.

Warm or cold limits

A common trend for all the target taxa, except *R. arboreum*, is that individuals seem to be able to grow outside the warm limit of the realized niche, but not the cold limit (Table 2). This also agrees with similar comparisons made on *Eucalyptus nitens* Dean and Maiden (Richardson and McMahon, 1992). This may indicate that heat stress is of minor importance as a limiting factor. Silvicultural data on evergreen conifers reveal that they grow best at their warm (southern) range limits (Korzukhin *et al.*, 1989; Bonan and Sirois, 1992). The reason for this may be that low temperatures in the temperate zone are directly linked to vital ecophysiological processes, whereas warm temperatures are more indirectly linked to moisture limitations, resistance to

pathogens, and competition (McArthur, 1972; Wright, 1976; Woodward and Williams, 1987). This is probably the underlying reason for the focus on cold-hardiness rather than heat tolerance in horticulture and forest sciences (e.g. Wright, 1976; Cox and Cox, 1997). Natural range limits often match with absolute minimum temperatures, and several studies have found that maximum frost resistance in evergreen broad-leaved trees is rarely below -15 °C (Sakai and Weiser, 1973; Woodward, 1996, 76 and references therein). Although similar growth forms may have common climate limits (Box, 1981) on a crude scale, the response to extreme low temperature (<-15 °C) is different among the rhododendrons, where *R. arboreum* and *R. barbatum* have an upper elevation limit where -15 °C hardly occurs, whereas *R. campanulatum* and *R. wallichii* reach an elevation (c. 4150 m a.s.l.) where <-15 °C may occur three times in a decade (Anonymous, 1995). Some broad-leaved evergreen species, such as *Quercus ilex* L., survive temperatures down to -24 °C (cf. Huntley *et al.*, 1995). This illustrates the individual species response to lethal limits within the same genus and even within the species as for the subspecies of *R. arboreum* (Vetaas, 2000b).

Although extreme temperatures are probably more related to the operating lethal factors than MAT (cf. Woodward and Williams, 1987; Gaines and Denny, 1993), this study found more correspondence between the realized and potential MAT niches than the MINCM and MAXWM niches. This is in contrast to a similar comparison in *E. citriodora* Hook., where only the realized MAT limits were extended (one exception) (Booth *et al.*, 1988).

Global warming relations

The present results demonstrate that extreme cold temperature may represent a hard boundary for tree species survival, whereas warm temperatures do not. Thus an increase in temperature as a result of global warming may not cause a dramatic die-back of rhododendron trees. This is in agreement with the hypothesis that several trees species may survive global warming *in-situ* because of high temperature tolerance (Loehle and LeBlanc, 1996; Schrenk, 1996). Although the trees will survive under increased temperatures, the long-term effect on their regeneration is uncertain. However, mild winters without frost may be problematic for their survival, if frosts are requisite for their seasonal growth rhythm. Qualitative information from several arboreta indicated that the major problem for rhododendron survival is too early growth during late winter/early spring followed by a sudden frost event. This may cause drought and will be lethally damaging to the trees. Lethal events are probably more common at the range boundaries (Huntley *et al.*, 1995) than at the centre and Kullman (1996) has, for instance, demonstrated rather rapid changes in the upper-limits of evergreen coniferous species. Global warming has taken place since the termination of the Little Ice Age (c. 1850 in the Himalayas; Röthlisberger, 1986), and one would expect a response in *R. arboreum* as it constitutes the warm boundary of the *Rhododendron* genera in the Himalayas.

There is no sign of reduced regeneration towards the warm limit, but its regeneration is mainly vegetative (O.R. Vetaas, unpublished data). Thus even if its sexual reproduction is reduced because of climate, it may continue to grow in this climate zone for very long periods, as *Tilia cordata* Mill has performed in England and Western Norway (Pigott and Huntley, 1981; Woodward, 1991). In lieu of this there may be a significant time lag between change in climate and transient species distribution (Wright, 1976; Woodward, 1991; Hengeveld, 1997). The pace of movement will depend on the longevity and dispersal ability of the species. As *Rhododendron* trees are relatively long-lived species, the individuals at low elevations may have survived from larger populations present during a cooler period (Vetaas, 2000a), such as the Little Ice Age (150–500 years BP) or other neoglaciation periods in the Himalayas (Röthlisberger, 1986). This possibility of a geographical separation of the actual regeneration limit and the limit of the realized range (Woodward, 1996; Hengeveld, 1997) makes the effect of global warming very difficult to predict for tree species.

Botanical gardens and arboreta are still a rather unused resource to elucidate potential effects of climate warming on plants. Although lack of certain species in a particular garden does not indicate that the target species are not able to grow there, the presence of species outside the realized niche does provide information on the potential niche. To establish the true limits for the potential niche more data are required on unsuccessful attempts, but such data are difficult to obtain as they often are caused by single events. Nevertheless this study shows that arboreta have useful information for scientists involved in climate change scenarios.

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BIOSKETCH

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Appendix I *Ex-situ* locations with latitude (lat), longitude (lon) (negative values indicate western- and southern-hemispheres), metres above sea level (m a.s.l.), precipitation (rain), mean annual temperature (MAT), mean minimum temperature of the coldest month (MIN), mean maximum temperature of the warmest month (MAX), moisture index (MI), *Rhododendron arboreum* (arbo), *R. barbatum* (barb), *R. campanulatum* (camp), and *R. wallichii* (walli)

<i>Ex-situ</i> locations	Lat	Lon	m a.s.l.	Rain	MAT	MIN	MAX	MI	arbo	barb	camp	walli
Akureyri, Iceland	65.7	-18.1	45	434	3.9	-2	11	1.9	0	0	0	0
Reykjavik, Iceland	64.1	-21.9	28	861	4.3	-2	14	2.9	0	0	1	0
Radoey, Bergen, Norway	60.7	50.0	43	1980	8.5	-2	22	4	0	1	0	0
Milde, Bergen, Norway	60.4	5.3	43	2002	8.3	-3	22	4.1	(+)	1	1	1
Uppsala, Sweden	59.8	17.6	24	554	5.1	-8	23	1.8	0	0	1	0
Tallin, Estonia	59.4	24.8	44	514	4.7	-9	21	1.9	0	0	1	0
Stockholm, Sweden	59.3	18.1	44	573	5.8	-6	21	1.7	0	0	1	1
Gotenberg, Sweden	57.7	12.0	17	776	7.5	-3	21	1.8	0	0	1	1
Wester Ross, UK	57.7	5.5	40	1603	8.9	2	18	3.1	1	1	1	1
Glendoick, Perth, UK	56.4	-3.5	60	760	8.0	1	17	1.6	1	1	1	1
Aarhus, Denmark	56.1	10.2	49	677	7.7	-3	21	1.5	0	1	1	(+)
Hoersholm, Denmark	55.9	12.5	30	603	8.5	-7	20	1.2	(+)	1	1	0
Edinburgh, UK	55.9	-3.2	134	703	8.7	2	18	1.4	1	1	1	1
Copenhagen, Denmark	55.7	12.5	13	584	8.0	-2	22	1.2	1	1	1	0
Ness, Liverpool, UK.	53.4	-3.1	60	637	9.6	2	19	1.3	1	1	1	0
Bremen, Germany	53.1	8.8	16	660	8.8	-1	22	1.3	1	1	1	1
Oldenburg, Germany	53.1	8.2	8	750	8.7	-4	21	1.5	1	0	0	0
Glasnevin, Dublin, Ireland	52.3	-6.2	20	724	9.8	2	19	1.3	0	0	1	0
Cambridge, UK	52.2	0.1	12	548	9.8	1	22	0.9	0	1	0	0
Münster, Germany	52.0	7.6	60	777	9.1	-2	23	1.4	0	0	1	0
Rogow, Warsaw, Poland	51.9	19.9	190	594	7.3	-20	23	1.4	0	0	(+)	0
Windsor Berkshire, UK	51.5	0.6	50	644	7.8	-3	22	1.4	1	1	1	1
Kew, Sussex, UK	51.5	0.0	45	584	10.3	2	23	1	1	1	1	1
Kent, UK	51.1	1.0	104	686	9.7	2	21	1.2	1	1	1	0
Brussels, Belgium	50.8	4.3	100	839	9.6	-1	23	1.5	(+)	0	1	1
Tharandt, Dresden, Germany	50.3	13.2	300	726	7.9	-3	24	1.6	0	0	1	1
Lviv, Ukraine	49.9	24.0	100	749	7.9	-8	23	1.6	(+)	(+)	(+)	1
Rouen, France	49.5	0.1	13	781	11.6	-1	23	1.1	1	0	0	0
Saarbrücken, Germany	49.3	7.0	252	796	9.0	1	15	1.5	0	0	1	0
Villers-Les-Nancy, France	48.7	6.2	233	719	9.4	-4	23	1.3	1	1	1	0
München, Germany	48.1	11.6	530	866	8.0	-5	22	1.8	0	0	1	1
Nogent Sur Vernisson, France	47.9	0.3	130	704	10.7	1	25	1.1	1/(+)	0	1	1
Fouesnant, France	47.9	-4.0	40	1212	11.4	4	22	1.8	1	0	0	0
Quimper, Elliant, France	47.9	-4.2	92	1212	11.4	4	22	1.8	1	1	1	1
Port Lodlow, WA, USA	47.8	-132.7	0	486	11.5	4	22	1.4	1	1	1	1
Federal Way, WA, USA	47.3	-122.3	30	980	10.5	6	15	1.6	1	1	1	1
Geneve, Switzerland	46.2	6.1	382	900	10.3	-2	25	1.5	1	1	1	1
East Lansing, MI, USA	42.7	-84.5	256	790	8.0	3	14	1.7	1	0	0	0
Duxbury, MA, USA	42.0	-72.0	20	1050	14	-15	28	1.3	0	0	1	0
Oyster Bay, NY, USA	40.9	-73.5	61	1057	11.6	-4	28	1.4	0	1	0	0
St Louis, MO, USA	38.8	-90.4	163	861	14.3	-8	32	1.2	(+)	0	0	0
Seta-Gun, Gunma, Japan	36.5	139.1	650	1470	10.9	-4	26	2.3	(+)	(+)	1	1
Mt. Tomah, NSW, Australia	-33.5	150.5	950	1351	13.1	0	26	1.8	0	0	1	0
New Plymouth, Taranaki, New Zealand	-39.3	-174.0	420	3550	11.6	2	26	4.3	1	1	1	1

Presence (1), absence (0) and died (+). Bold face indicates temperature outside the realized ranges of all the target rhododendrons.