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# Comparing species temperature response curves: population density versus second-hand data

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**Abstract.** Descriptions of individual species responses to temperature are required in order to assess the impact of future global warming. The response of *Rhododendron arboreum* to estimated mean annual temperature was investigated in the Himalayas using General Additive Models (GAM) and Generalized Linear Models (GLM). The aim was to evaluate the consistency between the response in population density along elevation gradients versus response curves based on elevation data from herbarium specimens and vegetation surveys. The comparison was made with respect to (1) estimated temperature at the point of maximum response and (2) the shape of the response curves i.e. symmetric vs skewed.

All data indicate a single optimum between 12.3 and 10.8°C. The difference is only 0.4°C between the optimum estimated from localities of herbarium specimens (frequency) and the population density data. The difference is larger (0.7°C) when the vegetation survey data are combined with the data from the herbarium specimens. However, the differences are small when the uncertainties in temperature estimation are taken into consideration. The response curves based on herbarium specimens and vegetation survey data (frequencies) are symmetric. A sigmoid response curve was estimated from herbarium specimens (binomial data). The population density along the elevation gradients was, to some extent, asymmetric. This may reflect the underlying biological structure, but sampling bias and the numerical analyses may also influence the results.

**Keywords:** Elevation gradient; Himalayas; Response optimum, *Rhododendron arboreum*; Skewness.

**Abbreviations:** GAM = General Additive Model; GLM = Generalized Linear Model; UTM = Universal Trans-Mercator.

## Introduction

The need for accurate descriptions of the performances of individual species in response to temperature has increased because of attempts to predict plant response to global warming and future climatic change (Austin 1992). It is a well accepted assumption that species abundance has a single optimum which decreases away from the optimum, either along a climatic gradient (Whittaker 1956; Gauch & Whittaker 1972; Jongman et al. 1987) or a biogeographical gradient (Shelford 1913; Hengeveld & Haeck 1982; Brown 1984).

The classical Gaussian optimum curve is, however, an idealized model and skewed and bimodal curves have been demonstrated by several authors (e.g. Whittaker 1967; Werger et al. 1983; Austin et al. 1984; Austin & Gaywood 1994). Most of the recent theories and hypotheses about response curves have been based on studies of large binary data sets at a biogeographical scale (Austin et al. 1990; Yee & Mitchell 1991; Austin & Gaywood 1994; Bio et al. 1998; Franklin 1998).

The general approach in such analyses is to convert second-hand data of species occurrence (e.g. distribution maps) into a binary data set (i.e. presence/absence) by superimposing a grid onto the distribution map. Climate data from the same grid-map can be used as predictors for the binary response variables by means of Generalized Linear Models (e.g. Austin et al. 1990). Recent concerns about global climate change have increased the need for information that can elucidate species-temperature relationships. Data compiled from herbaria, such as geocoded herbarium specimens including altitude, may be used to generate the first graphical approximation of a temperature response model for a species (Yee & Mitchell 1991: cf. Westman 1991). A binary data set can be obtained by using the presence of other species, e.g. in the same genus, as absence values. The idea of constraining the sample location to the occurrence of a genus has been used for niche estimation of *Eucalyptus* species, mainly based on data from *Eucalyptus* forest (Austin et al. 1990). This approach will also implicitly set the limits of the analysed gradient (cf. Austin & Nicholls 1997; Oksanen 1997), thus the genus should cover a large part of the target gradient.

However, it is not certain that response patterns estimated from herbarium data or other second-hand data are similar to a response curve based on population density along the same gradient at a smaller spatial scale (Westman 1991; Ferrer-Castan et al. 1995). This paper compares the response in population density along elevation gradients with response curves based on elevation data from herbarium specimens and vegetation surveys (i.e. second-hand data) in Nepal. To permit this comparison elevation is used to estimate the explanatory variable, i.e. mean annual temperature.

The gradient in this study is constrained by the occurrence of the genus *Rhododendron* in the central Himalayas (Nepal), the target species is *Rhododendron arboreum*. The data are from Nepal, which lies central to its geographical distribution range (Fig. 1). The species occurs as two subspecies in this region and may have a complex response curve difficult to describe by parametric regression (Yee & Mitchell 1991; Austin et al. 1994; Oksanen 1997; Austin & Nicholls 1997). To describe the shape of the response curve the non-parametric extension of Generalized Linear Models (GLM: Nelder & Wedderburn 1972) called General Additive Models (GAM: Hastie & Tibshirani 1990) was used. GAM allows the data to determine the shape of the response curve, but for the optimum estimation GLM (Yee & Mitchell 1991) was used.

Interpretation of the predicted probability of occurrence is conditioned by the fact that the temperature gradient is defined by the occurrence of the genus *Rhododendron*. This will bias the result for a species whose range reaches the end of the gradient, such as the target species here. The number of specimens documented for each 100 m interval was therefore also used as a response variable (see methods and discussion).

The main aim was to check if the temperature response based on second-hand data was comparable with the temperature response obtained from population density data. This was done with respect to (1) the temperature at the point of maximum response and (2) the shape of the response curve, i.e. symmetric *vs* skewed. The optima estimated from the regression models rely on the assumption of an error-free explanatory variable (Chatterjee & Hadi 1988), which is normally not the case in field ecology (Birks et al. 1990; Yee & Mitchell 1991). The difference between optima will be discussed in relation to the inevitable error in the temperature estimates, which also has a practical implication for the assessment of future changes in distribution.

## Material and Methods

### Geography and second-hand data sources

*Rhododendron arboreum* is a large species with a tree-type growth habit. Its distribution range follows the Himalayan mountain range from Kashmir (India) in the west to southwest China in the east (Fig. 1) (Chamberlain 1982), while there are also disjunct populations in southern India and Sri Lanka. The data from herbaria and vegetation surveys represent a part of this corridor along the Himalayan mountains (Fig. 1).

There are 141 specimens of *R. arboreum* in the herbarium data, which consist in total of 995 *Rhododendron* specimens (30 species) with elevation and UTM-location (Noshiro 1997). The herbarium data were also supplemented with data from vegetation surveys in *Quercus-* and *Abies* forests ranging from 2100 to 3450 m a.s.l. *R. arboreum* occupies the sub-canopy strata in these forests (Vetaas 1997; Vetaas & Chaudhary 1998; Maaren 1997; Dallard unpubl.). These data consist of 278 plots, 71 of which contain *R. arboreum*.

### Elevation gradients

The sampling of population density data took place along two elevation gradients in east Nepal from 1500 m a.s.l. up to 3600 m in (I) the Solu-Khumbu District (27° 30' - 50' N and 86° 40' - 50' E) and (II) at Milke Danda (27° 15' - 25' N and 87° 27' - 32' E) (Fig. 1). The choice of elevation gradient was based on the elevation range for *R. arboreum* found in the literature: 1850-3650 m a.s.l. (Chamberlain 1982) and 1500-3600 m a.s.l. (Hara et al. 1982).

The upper parts of the gradients (> 2900 m a.s.l.) have a cool temperate climate, a warm temperate climate is found at lower elevations. The climate station
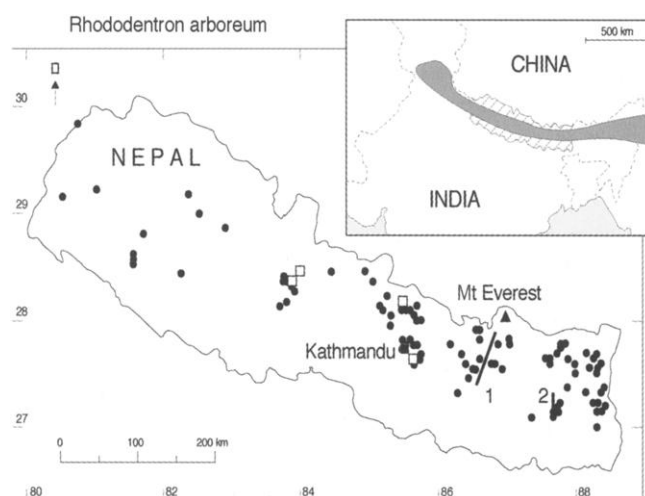


**Fig. 1.** Map showing the distribution of *Rhododendron arboreum* in the Himalayas and the location of herbarium specimens (●) (Noshiro 1997), elevation gradients (1 and 2) and vegetation survey areas in Nepal (□). Kathmandu (■) and Mt.-Everest (▲) are also shown. Coordinates are degrees longitude E (X-axis) and latitude N (Y-axis)

closest to the lowest sampling points has a mean annual temperature of 16.4 °C (Okladunga at 1720 m) in area (I) and 16.0 °C in area (II) (Tapeljung at 1768 m). The highest stations have an annual mean of 3.9 °C in area (I) (Tengboche at 3800 m) and 7.6 °C in area (II) (Wallung-chola at 3048 m). The region has a monsoon climate where 80% of the precipitation falls during the summer season (May to October) (ca. 1000-3000 mm/yr). However, short showers are common during winter, falling as snow above 2300 m a.s.l.

The forests along the gradient from 1500 m to 2900 m are classified as 'Low to Mid-Montane Hemi-Sclerophyllous Broadleaf Forest' (Singh & Singh 1987). The canopy dominants are evergreen oak trees such as *Quercus glauca*, *Q. lanata*, *Q. lamellosa* and *Q. semecarpifolia*, with a sub-canopy layer of rhododendrons including *R. arboreum, R. barbatum, R. wallichi, R. campanulatum* and phanerophytes belonging to the *Lauraceae* (Dobremez 1976; Vetaas & Chaudhary 1998). Above 2900 m a.s.l. there is woodland dominated by *Abies spectabilis, R. campanulatum, R. wallichi* and shrubs dominated by *Juniperus* spp. (Dobremez 1976).

The area can be regarded as a cultural landscape where the forests are often 'islands' in a matrix of cultural activities, such as agriculture and grazing. Therefore the forest sampled was of different sized patches, often adjacent to vegetation modified by human activity (Vetaas 1997).

*Population density sampling*

103 plots of 0.1 ha were sampled in area (I) (spring 1997) and 91 plots in area (II) (spring 1998). Four or five plots were sampled at each 100 m elevation interval. The first plot was selected in the forest adjacent to a well-established footpath and included a mature tree type rhododendron. This was used as the centre point of the first plot at a pre-defined elevation interval (e.g. 1500-1600 m). The remaining plots were at the same elevation and were separated by a minimum distance of 30 m. Due to inaccessible terrain (i.e. inclination > 50 %) the distance between the plots varied from 30 to 200 m. The number of individuals, including saplings and seed-lings, in each plot was counted. Where these tree type rhododendrons were not observed from the footpath at a certain elevation, a search was conducted on either side of the path. Zero population density was recorded when *R. arboreum* was absent in a plot inhabited by another tree type rhododendron or if no tree type rhododendrons were found. The physical variables measured were (1) slope inclination and (2) aspect, which were combined into a Radiation Index, $RI = f$ (aspect, inclination, latitude) (Oke 1987: 339-348) and (3) altitude measured with an altimeter. The starting points were calibrated using a contour

map, and each new sample was related to the one below to reduce estimation error (cf. Beals 1969).

*Temperature estimation*

A national lapse rate based on data from all over Nepal (Anon. 1998; cf. Dobremez 1976) was used to estimate the temperature for each 100 m interval. The lapse rate predicts a decrease of 0.51 °C/100 m. The starting point for the interpolation was 12.6 °C at 2350 m a.s.l., which is the mean elevation and temperature for the 10 climate stations closest to the areas where population density data were collected (Fig. 1). A scatter plot between potential radiation and elevation revealed a change in microclimate habitat along the elevation gradients. Area (I) had enough rainfall stations to allow estimation of mean annual rainfall for each elevation interval (100 m).

*Numerical analyses*

Geocoded herbarium data are seldom used to esti-mate the temperature responses of species (but see Yee & Mitchell 1991). There are several potential problems in this approach. 1. The herbarium specimens (as most second-hand data) are not a random sample, but the original collections were independent of the current research question. In this study the data cover the full elevation range. Checking that spatial temperature-el-evation gradient is completely sampled is much easier than for other environmental gradients which are less unidirectional and continuous in space. 2. The approach relies on the assumption that the number of individuals collected are proportional to the species abundance along the elevation range. However, in areas where the flora is well documented, collectors tend to collect taxa where they are locally rare, resulting in a bias towards mar-ginal locations. In the Himalayas this is assumed to be a minor problem at present. There is a possibility of incomplete sampling (Kodric-Brown & Brown 1993), but this is less likely for woody perennials than for rare herbaceous species (cf. Box et al. 1993).

The herbarium data were first treated as a binomial variable, i.e. presence of *R. arboreum* and absence (= *Rhododendron* taxa other than *R. arboreum*). Since the target species has the lowest occurrence of *Rhododendron* specimens in Nepal the predicted probability of occurrence will be biased (see Discussion). Therefore the response variable was transformed to the number of specimens documented for each 100 m interval. Only the optimum based on the second-hand data (i.e. her-barium data and survey data) were compared with the population density data.

The population density data and the second-hand

data were both analysed with General Additive Models (GAM: Hastie & Tibshirani 1990) to estimate response curves with estimated temperature as predictor (cf. above). The population density data were square-root transformed, to reduce over-dispersion in the regression analyses (Snedecor & Cochran 1980). 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). The response curve for area (I) was also estimated after correcting for *RI* and estimated rainfall:

corrected response = measured response – estimated response

with *RI* and rainfall as predictors.

The skewness of the predicted GAM responses was evaluated graphically by superimposing a symmetric Gaussian response on the same figure. The Gaussian response was calculated according to the formula given by ter Braak & Looman (1987:42), with the same optimum temperature as the GAM response and the tolerance set to a quarter of the range found in Table 1.

Optima extracted from the GAM curves are limited to the temperatures given by the lapse rate at each 100 m interval. Therefore GLM was used to estimate optimum temperature as it allows the optima to have values between the lapse rate intervals (cf. Yee & Mitchell 1991) [optimum= $-b_1/2b_2$, where $b_1$ and $b_2$ are first and second order polynomial coefficients, ter Braak & Looman (1987:42)]. An approximate confidence interval for the optimum can be estimated from the polynomial coefficients ($b_1$ and $b_2$) and their correlation-covariance matrix (Finney 1964: 27-29, ter Braak & Looman 1987). All GAM and GLM analyses were made with both an assumed Gaussian and a Poisson error distribution. The Anscombe residual from each test was compared by drawing a diagnostic Q-Q-plot (Chambers & Hastie 1993). This indicated that the Poisson model was best for GLM and the Gaussian for GAM. Thus the exponential polynomials were used with a log-link function in GLM, and identity link in GAM. All analyses were performed using the *S*-Plus program version 3.3 (Anon. 1993).

**Table 1.** Response of *Rhododendron arboreum* to mean annual temperature. Estimated optima of the population density (Nr. of individuals/0.1 ha) with 95 % Confidence Interval (CI) based on GLM. Max and Min are observed limits.

| Data sets | Optimum ± CI | Max | Min |
|---|---|---|---|
| (I) Solu-Khumbu | 12.3 ± 0.49 | 16.7 | 6.5 |
| (II) Milke Danda | 10.8 ± 0.24 | 14.7 | 7.5 |
| (I) and (II) | 11.7 ± 0.24 | 16.7 | 6.5 |
| Herbarium data: frequency | 11.3 ± 0.55 | 19.4 | 4.5 |
| As above + survey data | 11.0 ± 0.37 | 19.4 | 4.5 |
| Herbarium data: binary | 19.4 | 19.4 | 4.5 |

## Results

### Response optima and limits

The midpoint based on the elevation range in the literature (1500 - 3600 m) (Hara et al. 1982, Chamberlain 1982) is equivalent to a temperature of 11.6 °C (2550 m) if a symmetric Gaussian response is assumed. All data sets indicate a single optimum (Fig. 2). The estimated optima based on the population density data are 10.8 and 12.3 °C (Table 1). These two models are different, indicated by the graph (Figs. 2e and 2g) and significant different regression coefficients ($b_1$ : F = 18.3 and $b_2$: F = 27.5). The optimum estimated from herbarium data (11.3 °C) is between the two optima estimated from the population density data. The optimum estimated from the two population density data sets combined (11.7 °C) is only 0.4 °C different from the estimate based on herbarium specimens. The difference is larger (0.7 °C) when the vegetation survey data are combined with the herbarium specimens data. The confidence interval for the optima is less than the change in temperature of ± 100 m elevation interval (cf. lapse rate), except for the optimum based only on herbarium data (Table 1).

The ranges shown in Table 1 are the estimated temperatures at the highest and lowest observations of *R. arboreum* for each data set. *R. arboreum* distribution was continuous from 1500 to 3600 m a.s.l. in area (I) but was absent from 1500-1800 m a.s.l. and 3400-3600 m a.s.l. in area (II). The elevation range is much wider for the herbarium observations than the elevation gradients. The highest herbarium observation is at 3950 m a.s.l. (4.5 °C) and the lowest at 1050 m a.s.l. (19.4 °C). The herbarium data are in partial agreement with recent literature (Cox & Cox 1997). The relationship between elevation and *RI* shows that high radiation is common for plots at higher elevation and *vice versa* at lower elevation (Fig. 3c).

### Response shape

*R. arboreum* showed no sign of a bimodal structure in response to temperature in any of the data sets. A clear unimodal response was found for all data sets, except for the binomial herbarium data. Here, a sigmoid response shape was estimated (Fig. 2a) which indicates that the probability of finding *R. arboreum* is highest at low elevations given that the genus *Rhododendron* occurs. All the unimodal responses were confirmed in GLM by a highly significant second-order polynomial and a non-significant third-order polynomial. The second-hand data have a symmetric response curve signified by the closeness between the GAM and Gaussian curves (Figs. 2b and 2c).
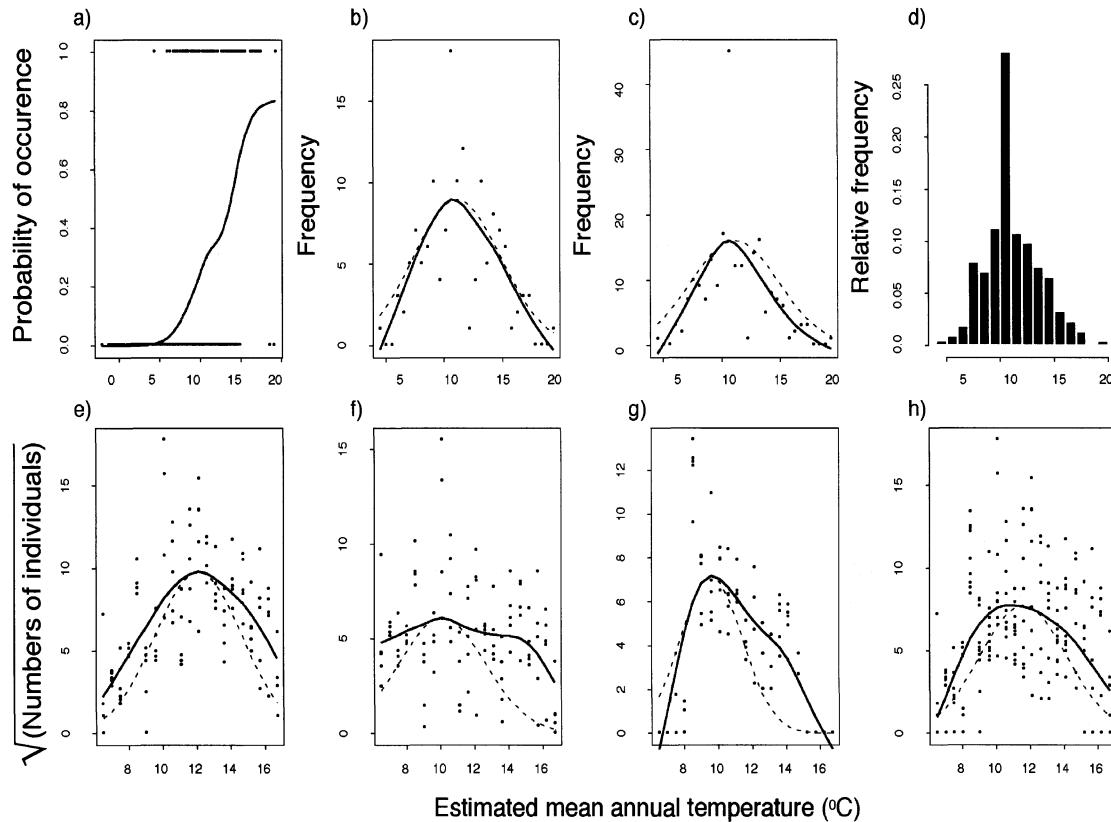
**Fig. 2.** Response curves for *Rhododendron arboreum* estimated with General Additive Models on different data (**a**) herbarium specimens: binary data, (**b**) herbarium specimens: frequency for each 100 m interval, (**c**) as (**b**) plus vegetation survey data, (**d**) probability histogram of estimated temperatures in (c), (**e**) square root of population density along elevation gradient (1), (**f**) as (e) but corrected for radiation index and estimated annual rainfall, (**g**) as (e) for elevation gradient (2) and (**h**) both elevation gradients together. The degree of skewness is illustrated by a Gaussian response curve (punctuated line) with similar optimum and range as the response curve.
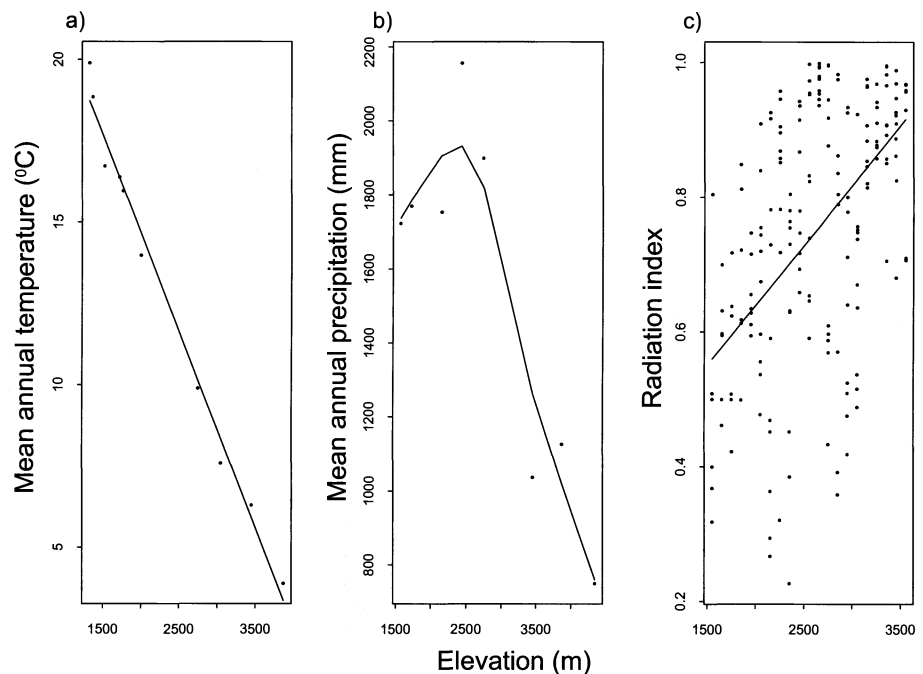


**Fig. 3.** Relationship between elevation and (**a**) mean annual temperature along the elevation gradients ($r = -0.99$); (**b**) rainfall in area (1) with GAM-smoother; (**c**) Radiation index ($r = 0.53$).

The population density data from area (I) and the population density data combined appear symmetric, but slightly different from the Gaussian curve (Figs. 2e and 2h). A clear positive skewed curve with the tail towards the warmer end of the gradient is found in area (II) (Fig. 2g). The skew is most obvious when the regression model is corrected for RI and estimated rainfall as for area (I) (Fig. 2f).

## Discussion

### Optima

The interpretation of the population density optima is biologically clear, but these optima may differ from the temperature interval where maximum cover of *R. arboreum* is found. This is because a low number of recruits is found in pure *R. arboreum* forest. The interpretation of optima based on frequency per 100 m interval is, however, not clear cut. This is seen in Fig. 2d, which shows that if *R. arboreum* occurs, the temperature is most probably 11.0 °C. The real meaning of probability and relative frequency is a matter of philosophical debate (Wonnacott & Wonnacott 1977). However, if one accepts the assumption that the number of specimens collected is proportional to the abundance of *R. arboreum* along the elevation gradient then the ecological meaning is that the optimum will be close to 11.0 °C.

The difference in optima between this first approximation based on second-hand data and population density data is very small. The reason for this may relate to two phenomena: 1. *R. arboreum* is a large species which is easy to observe and is common in the sampling area. This reduces the chances of incomplete sampling (Brown 1984; Kodric-Brown & Brown 1993). However, the elevation range for the population density data is to some extent incomplete as the elevation range found in the herbarium data is greater (Table 1); (2) Temperature is probably one of the best predictors of plant distribution (Woodward 1987) and is operative at different spatial scales (Woodward & Williams 1987). Although mean annual temperature is not an operational factor for plant survival (Woodward & Williams 1987; Woodward 1997), it is probably highly correlated with the ecophysiological conditions under which plants generally survive. In this study the optimum corresponds to an elevation at which there is a relatively high annual rainfall (Fig. 3b). Rainfall is a very important factor and explains 39% of the deviance in the model from area (I), which is almost the same as the deviance explained by temperature as a single factor in both areas (Table 2).

The temperature-elevation gradient is probably one of the most continuous ecological gradients at a large

scale. However, the variation in potential solar radiation at the same elevation interval illustrates indirectly the discrepancy between actual and estimated temperatures (Neilson et al. 1992). The interpolated temperature at the location of the plot or specimen may also be inaccurate due to the residual standard error of the lapse rate model (1.0 °C Anon. 1998). In addition, rapid change in air pressure in mountainous areas causes errors in estimating elevation, but the error is probably less than one elevation interval (100 m a.s.l. = 0.51 °C) since each new sampling interval was related to the one below. The discrepancy between the optima (Table 1) is very small if one takes all these uncertainties into consideration. Consequently it is legitimate to express the temperature optimum of *R. arboreum* as an interval of 12.3 to 10.8 °C, rather than an exact value (e.g. 11.5 °C, the midpoint between the two main predictions) (Table 1). An optimum interval is in accordance with the idea of a dynamic optimum which alternates over generations within a given interval (Gaston 1990; Hengeveld 1997; Shugart 1998), where the pace of movement will depend on the longevity of the species. On the other hand optima expressed as intervals rather than exact values will complicate the attempt to predict future changes in biogeographical distribution as a result of global changes (e.g. Huntley et al. 1995; Saetersdal & Birks 1997; Franklin 1995 and references therein).

### Response shape

Two subspecies of *R. arboreum* are found in Nepal and a bimodal response curve might therefore be expected (Whittaker 1967) but this was not found (but see Vetaas 1998). The sigmoid response based on the binomial herbarium data is an artefact because *R. arboreum* has the highest temperature limits of all the *Rhododendron* species in the data. Many absence values beyond the minimum temperature and a lack of absence values higher than maximum temperature cause an ecologically invalid response shape (Fig. 2a). This

**Table 2.** Regression statistics for the models in Fig. 2.

| Fig. | Dev | df | Term | Res-Dev | Res df | % Dev-Expl | Chi(p) |
|------|-----|----|----|----|----|----|----|
| 2b | 543.3 | 29 | s(temp) | 231.7 | 24.9 | 50 | p < 0.001 |
| 2c | 2269.4 | 29 | s(temp) | 1156.5 | 24.9 | 41 | p < 0.001 |
| 2e | 1342.9 | 102 | s(temp) | 765.5 | 97.9 | 41 | p < 0.001 |
| 2g | 1062.6 | 90 | s(temp) | 406.6 | 85.9 | 60 | p < 0.001 |
| 2h | 2820.2 | 193 | s(temp) | 1966.2 | 188.9 | 29 | p < 0.001 |
| 2f | 1342.9 | 102 | s(rain) | 788.9 | 97.9 | 39 | p < 0.001 |
|  |  |  | s(ri) | 735.3 | 92.9 | 3 | p < 0.001 |
|  |  |  | s(temp) | 586.7 | 89.9 | 17 | p < 0.001 |

Dev = Total Deviance; Res-Dev = Residual Deviance; % Dev-Expl = percent Deviance explained; $\chi$ (p) = probability of the $\chi$-test; s(temp) = smooth function of mean annual temperature; rain = mean annual rainfall; ri = radiation index – s(ri) is not significant if the F-test is used.

illustrates the problems related to the interpretation of 'probability of occurrence' for a species whose range reaches the end of the gradient, especially when there are no other co-analysed species, as in this study. The interpretation may be legitimate when two or more species reach the end of a primary gradient, as shown by Yee & Mitchell (1991), but the response curve close to the end point is still strongly influenced by the degree of absence values given by other co-analysed species. To avoid this only species with a certain number of zero observations beyond the lowest or highest positive observation should be included (Austin et al. 1994; Franklin 1998).

A different approach is to use only presence values, i.e. frequencies per elevation interval. This gave a symmetric response curve (Fig. 2b and c). However, species responses along a given ecological variable may simply appear as frequency distributions of that particular ecological variable if only presence values are included (see above) (Kershaw & Looney 1985: 29). The interpretation of response shapes based on population density are preferred because they are independent of the frequency of the predictor. This is because the sampling intensity along the elevation gradient is almost uniform. This gave a more asymmetric response, where two models have tails towards the warmer end of the gradient (Fig. 2f, g). According to the conceptual model by Austin & Gaywood (1994) the tail should have been towards the colder end of the gradient since the optimum of *R. arboreum* (11.5 °C) is located at the warmer end of the temperature gradient. This latter location is true when the gradient is constrained by the occurrence of *Rhododendron* (-1.3 to 19.8 °C) or by the occurrence of vascular plants (-8.6 to 24.8 °C) in Nepal. However, the direction of the tail may be a consequence of the elevation itself. A tail towards high temperature (low elevation) may be caused by a down-slope distribution of seeds (cf. Beals 1969; Hengeveld 1985). Since *R. arboreum* is a long-lived species individuals at low elevations may have survived from larger populations present during a cooler period, such as the Little Ice Age or other neoglaciation periods in the Himalayas (Röthlishberger 1986). This may illustrate that the asymmetric responses are a result of an underlying biological process, but sampling bias and the numerical treatment used may also have influenced the result (Austin et al. 1984; Yee & Mitchell 1991).

However, it is revealing that the optima intervals are similar for data sampled at different spatial scales and very different biological sampling resolutions. The results suggest that data from herbarium specimens across an elevation range can be compared with population density data along that range, but the approach is probably best for perennial species which are easily recognized and relatively common.

## References

Anon. 1993. Statistical Science. *S-plus for Windows. Version. 3.2.* StatSci. A division of Mathsoft, Inc., Seattle.

Anon. 1998. *Seasonal variation of temperature lapse rate (°C/ 1000 metre) for Nepal.* HMG Department of Hydrology and Meteorology, Kathmandu. (Unpubl. note.)

Austin, M.P. 1992. Modelling the environmental niche of plants: implications for plant community response to elevated $CO_2$. *Aust. J. Bot.* 40: 615-630.

Austin, M.P. & Gaywood, M.J. 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. *J. Veg. Sci.* 5: 473-482.

Austin, M.P. & Nicholls, A.O. 1997. To fix or not to fix the species limits, that is the ecological question: Response to Jari Oksanen. *J. Veg. Sci.* 8: 743-748.

Austin, M.P., Cunningham, R.B. & Flemming, P.M. 1984. New approach to direct gradient analysis using environmental scalars and statistical curve-fitting procedures. *Vegetatio* 55: 11-27.

Austin, M.P., Nicholls, A.O. & Margules, C.R. 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.* 60: 161-77.

Austin, M.P., Nicholls, A.O., Dohherty, M.D. & Meyers, J.A. 1994. Determining species response functions to an environmental gradient by means of a beta-function. *J. Veg. Sci.* 5: 215-228.

Beals, E.W. 1969. Vegetational change along altitudinal gradients. *Science* 165: 981-985.

Bio, A.M.F., Alkemade, R. & Barendregt, A. 1998. Determining alternative models for vegetation response analysis: a non-parametric approach. *J. Veg. Sci.* 9: 5-17.

Birks, H.J.B., Line, J.M., Juggins, S., Stevenson, A.C. & ter Braak, C.J.F. 1990. Diatom and pH reconstruction. *Phil. Trans. R. Soc. Lond.* B 327: 263-278.

Box, E.O., Crumpacker, D.W. & Hardin, D.E. 1993. A climate model for location of plant species in Florida, U.S.A. *J. Biogeogr.* 20: 629-644.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255-279.

Chamberlain, D.F. 1982. Revision of *Rhododendron* II - subgenus *Hymenanthes. Notes R. Bot. Garden Edinb.* 39 (2).

Chambers, J.M. & Hastie, T.J. (eds.) 1993. *Statistical models in S.* Chapman & Hall, London.

Chatterjee, G. & Hadi, A.S. 1988. *Sensitivity analysis in linear regression.* John Wiley & Sons, NY.

Cox, P.A. & Cox, K.N.E. 1997. *The encyclopaedia of Rhododendron species.* Glendoick Publ., Perth.

Dobremez, J.F. 1976. *Le Népal: Ecologie et biogéographie.* Centre National de la Rechereche Scientifique, Paris.

Ferrer-Castan, D., Calvo, J.F., Esteve-Selma, M.A., Torres-Martinez, A. & Ramirez-Diaz, L. 1995. On the use of three performance measures for fitting species response curves. *J. Veg. Sci.* 6: 57-62.

Finney, D.J. 1964. *Statistical methods in biological assay.* Griffin, London.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progr. Phys. Geogr.* 19: 474-499.

Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain derived variables. *J. Veg. Sci.* 9: 733-748.

Gaston, K.J. 1990. Patterns in the geographical ranges of species. *Biol. Rev.* 65: 105-129.

Gauch, H.G. & Whittaker, R.H. 1972. Coenocline simulation. *Ecology* 53: 446-451.

Hara, H., Chater, A.O. & Williams, H.J. 1982. *An enumeration of the flowering plants of Nepal, Vol. III.* British Museum Natural History, London.

Hastie, T.J. & Tibshirani, R.J. 1990. *Generalized additive models.* Chapman & Hall, London.

Hengeveld, R. 1985. On the explanation of the elevation effect by a dynamic interpretation of species distribution along altitudinal gradients. *Blumea* 30: 353-361.

Hengeveld, R. 1997. Impact of biogeography on a population-biological paradigm shift. *J. Biogeogr.* 24: 541-547.

Hengeveld, R. & Haeck, J. 1982. The distribution of abundance I. Measurements. *J. Biogeogr.* 9: 303-316.

Huntley, B., Berry, P.M., Cramer, W. & McDonald, A.P. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. *J. Biogeogr.* 22: 967-1001.

Kershaw, K.A. & Looney, J.H.H. 1985. *Quantitative and dynamic plant ecology.* 3rd ed. Arnold, London.

Kodric-Brown, A. & Brown, J.H. 1993. Incomplete data sets in community ecology and biogeography: a cautionary tale. *Ecol. Appl.* 3: 763-742.

Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. 1987. *Data analysis in community and landscape ecology.* Pudoc, Wageningen.

Maaren, I.E. 1997. *Community and population dynamics in Quercus semecarpifolia forest along a disturbance gradient in the Annapurna Area, Nepal.* Thesis University of Bergen.

Neilson, R.P. King, K.A., DeVelice, R.L. & Lenihan, J.M. 1992. Regional and local vegetation patterns: the response of vegetation diversity to subcontinental air masses. In: Hansen, A.J. & di Castri, F. (eds.) *Landscape boundaries,* pp. 129-149. Springer, New York, NY.

Nelder, J.A. & Wedderburn, R.W.M. 1972. Generalized linear models. *J. R. Stat. Soc.* 135: 370-380.

Noshiro, S. 1997. Distribution maps of *Rhododendron* in Nepal. *Newslett. Himalayan Bot.* 21: 21-28.

Oke, T.R. 1987. *Boundary layer climates.* Methuen, London.

Oksanen, J. 1997. Why the beta-function cannot be used to estimate skewness of species responses. *J. Veg. Sci.* 8: 147-152.

Röthlishberger, F. 1986. *10000 Jahre Gletschergeschichte der Erde.* Verlag Sauerlander, Aarau.

Saetersdal, M. & Birks, H.J.B. 1997. A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *J. Biogeogr.* 24: 127-152.

Shelford, V. E. 1913. *Animal communities in temperate America.* Chicago University Press, Chicago, IL.

Shugart, H.H. 1998. *Terrestrial ecosystems in changing environments.* Cambridge University Press, Cambridge.

Singh, J.S. & Singh, S.P. 1987. Forest vegetation of the Himalaya. *Bot. Rev.* 53: 80-192.

Snedecor, G.W. & Cochran, W.G. 1980. *Statistical methods.* 7th ed. Iowa University Press, Iowa, IA.

ter Braak, C.J.F. & Looman, C.W.N. 1987. Regression. In: Jongman, R.H.G., ter Braak, C.J.F. & van Tongeren, O.F.R. (eds.) *Data analysis in community and landscape ecology,* pp. 29-77. Pudoc, Wageningen.

Vetaas, O.R. 1997. The effect of canopy disturbance on species richness in central Himalayan oak forest, Nepal. *Plant Ecol.* 132: 29-38.

Vetaas, O.R. & Chaudhary, R.P. 1998. Scale and species-environment relationships in central Himalayan oak forest, Nepal. *Plant Ecol.* 134: 67-76.

Vetaas, O.R. 1998. Separation of sub-species along a temperature gradient. In: Sjøgren, E., van der Maarel, E. & Pokarzhevskaya, G. (eds.) *Stud. Plant Ecol.* 20: 9.

Werger, M.J.A., Louppen, J.M.W. & Eppink, J.H.M. 1983. Species performance and vegetation boundaries along an environmental gradient. *Vegetatio* 52: 141-150.

Westman, W.E. 1991. Measuring realized niche space: climatic response of chaparral and coastal sage scrub. *Ecology* 72: 1678-1684.

Whittaker, R.H. 1956. Vegetation on Great Smoky Mountains. *Ecol. Monogr.* 26: 1-80.

Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 49: 207-264.

Wonnacott, T.H. & Wonnacott, R.J. 1977. *Introductory statistics.* 3rd ed. Wiley, New York, NY.

Woodward, F.I. 1987. *Climate and plant distribution.* Cambridge University Press, Cambridge.

Woodward, F.I. 1997. Life at the edge: a 14-year study of a *Verbena officinalis* population's interaction with climate. *J. Ecol.* 85: 899-906.

Woodward, F.I. & Williams, B.G. 1987. Climate and plant distribution on global and local scale. *Vegetatio* 69: 189-197.

Yee, T.W. & Mitchell, N.D. 1991. Generalized additive models in plant ecology. *J. Veg. Sci.* 2: 587-602.