Separation of subspecies along a temperature gradient

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Abstract. The conceptual niche model is implicit in several theories in vegetation science, population ecology, biosystematics and speciation. Whittaker and Austin have demonstrated that the response of a single species to environmental gradients can explicitly link the conceptual models of a vegetation continuum and the realized niche of a species. Whittaker has suggested that a bimodal response may indicate segregation in subpopulations with distinct genetics (ecotypes). This study used General Additive Models (GAM) and Generalized Linear Models (GLM) to evaluate if two interbreeding taxa (*Rhododendron arboreum* ssp. *arboreum* and ssp. *cinnamomeum*) had two distinct realized niches with respect to temperature. The species *Rhododendron arboreum* did not have a bimodal response to temperature. The two subspecies increased from either end of the temperature gradient towards the middle, when plots in which the taxa were actually growing were analysed. Only ssp. *arboreum* showed a weak unimodal response to temperature. Both subspecies showed unimodal responses to temperature when plots where the target taxa did not occur were included in GLM and GAM. The ecological or biosystematic interpretation depend on the numerical approach, which illustrate the problem of formalizing the conceptual niche concept. This demonstrates that the development of vegetation theory is lagging behind the rapid advances in numerical techniques.

Keywords: Elevation gradient**,** Himalaya, Nepal, Niche separation, *Rhododendron arboreum.*

Introduction

The bell-shaped response curve for species along environmental variables is a well- excepted model in vegetation theory (Whittaker 1956; Gauch & Whittaker 1972; Jongman et al. 1987). Whittaker (1956, 1967) and Austin (1985) have argued that such response curves can be viewed as a unidimensional realized niche of a species. This may bridge the conceptual models of a vegetation continuum with biosystematics theory. A proper ecological niche is one of the characteristics of a biologically defined species (*sensu* Mayr 1982), and is the main criterion for the ecological species concept (*sensu* van Valen 1976; Andersson 1990).

The Gaussian optimum curve is, however, an idealized model, and asymmetric and bimodal curves have been demonstrated by several authors (Whittaker 1967; Werger et al. 1983; Austin et al. 1990; Bio et al. 1998). Whittaker (1967) has suggested that deviation from a unimodal bell-shaped response, such as bimodal, may indicate segregation

in subpopulations with distinct genetics, (ecotypes or subspecies). Bimodality is, however, not so easy to detect with the curve fitting procedure currently applied, such as Generalized Linear Models (GLM: Nelder & Wedderburn 1972; Austin et al. 1990). In this respect the non-parametric extension of GLM, Generalized Additive Models (GAM: Hastie & Tibshirani 1990) is an improvement since it allows the data to determine the shape of the response curve. Thus bimodality or asymmetry can easily be detected.

This study aims to evaluate if two subspecies of *Rhododendron arboreum* have distinct realized niches with respect to temperature. This was done by checking for (1) a bimodal structure in *R. arboreum* and (2) a bell-shaped unimodal response in the two subspecies. The effect of including plots where the target taxa do not occur is discussed in relation to the ecological and biosystematical interpretation.

Material and Methods

Area and taxa

The sampling took place along an elevation gradient from 1500 m a.s.l. up to 3600 m following the Dudh Kkoshi river in the Solu-Khumbu District in East Nepal (27° 30' -50' N and 86° 40' -50' E). The upper part of the gradient (> 3200 m a.s.l.) is within the Mt. Everest National park and has a cool temperate climate, whereas a warm temperate climate is found at lower elevation. The area has a monsoon climate where 80% of the precipitation falls during the summer season (May to October) (ca. 1000 -2000 mm/yr). However, short showers are common during winter, falling as snow above 2300 m a.s.l.

The climate station closest to the lowest sampling point (Okladunga at 1720 m a.s.l.) has a mean annual temperature of 16.4°C, and average minimum and maximum temperatures of 5.4 °C (January) and 23.1°C (July) respectively. The highest station (Tengboche at 3800 m a.s.l.) has an annual mean of 3.9 °C, and average minimum and maximum temperatures of –10.1 °C and 14.3 °C respectively.

The forests along the gradient from 1500 m a.s.l. to 2900 can be 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*, *O. lamellosa* and *Q. semecarpifolia,* with a subcanopy layer of *Rhododendron arboreum* Sm. and phanerophytes belonging to the *Lauraceae* (cf. Dobremez 1976; Vetaas & Chaudhary 1997). Above 2900 m a.s.l. there is woodland dominated by *Abies spectabilis, Rhodendron arboreum*, *R. wallichi* and shrubs mainly *Juniperus* spp. (Dobremez 1976).

The area can be regarded as a cultural landscape where the forests are often 'islands' in a matrix of fields and grasslands. The forest patches sampled were of varying size and often situated adjacent to vegetation modified by human activity.

Rhododendron arboreum is a large tree-forming *Rhododendron* in the subgenus *Hymenanthes*. The two target subspecies, *R. arboreum* ssp. *arboreum* and ssp. *cinnamomeum*,

have different indumentum on the lower surface of the leaves. Spp. *arboreum* has a silvery to grey compacted indumentum and ssp. *cinnamomeum* has a loose indumentum with a brown to dark rusty brown colour (Chamberlain 1982). Biogeographically the subspecies differ: ssp. *arboreum* is most common in the western Himalaya and ssp. *cinnamomeum*, in the eastern. Their distributions overlap in East Nepal and adjacent India and Bhutan, where ssp. *arboreum* is more common at lower elevations and ssp. *cinnamomeum* higher up.

Sampling and analyses

A total of 103 plots of 0.1 ha were sampled in the spring of 1997 in the valley which leads to Mt. Everest base camp. Due to topography and the cultural activity it was not possible to sample all 100 m intervals systematically along one transect (slope). Thus a sequence of 100 m intervals may not necessarily be geographically close, which breaks the continuous relation between geographical space and elevation/temperature as in classical direct gradient analyses (Whittaker 1967). Five plots were sampled at each 100-m interval according to the following scheme: a mature *Rhododendron arboreum* in the forest adjacent to a well-established footpath was used as the middle point of the first plot at a pre-defined elevation interval (e.g. 1500-1600 m, etc.). This plot was used as the starting point for the subsequent four plots, which should be at the same elevation with a minimum horizontal distance of 30 m between. Due to inaccessible terrain (e.g. inclination > 50 %) the distance between the plots varied from 30 to 200 m. The number of individuals were counted in each plot, and the altitude noted. A local temperature lapse rate was estimated (five stations) to be 0.56 °C per 100 m – the national lapse rate for annual mean temperature is 0.51 °C (cf. Dobremez 1976).

Numbers of individuals were square-root transformed prior to regression analysis in order to reduce overdispersion. Two analyses were made for each taxon; with and without plots where the target taxon did not occur. General Additive Models (GAM: Hastie Tibshirani 1990) were used to determine whether *R. arboreum* has a bimodal response to temperature. The same method was used to check if the two subspecies have a unimodal (bell-shaped) response. A cubic spline smoother (4 df) 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.

If bimodal or unimodal responses were detected parametric tests were made using Generalized Linear Models (GLM; McCullagh & Nelder 1989). Unimodality was evaluated by testing the significance of a model including a second order term against a linear model. Bimodality was evaluated by testing the significance of a model including a third and fourth order term against a unimodal model. Overdispersion was generally high; this means that an *F*-test (Chambers & Hastie 1993) is required.

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, although the differences were not large in either analysis. All analyses were performed using the S-plus program version 3.3 (Anon. 1993).

Results and Discussion

There was no sign of a bimodal structure in the response curve to temperature when the two subspecies were analysed together with GAM (*R. arboreum*) (Fig. 1). A clear unimodal response was confirmed in GLM by a highly significant second-order polynomial and a nonsignificant third order polynomial. A slight skewness (not significant) will appear in Fig. 1 if the data were not square-root transformed and analysed with a log-link function (Poisson error).

Subspecies *arboreum* has a unimodal response to temperature in the GAM analyses where absence values were excluded, but subspecies *cinnamomeum* has a positive log-linear trend (Fig. 2a, c). The significance of the unimodal response in GAM of ssp. *arboreum* (Fig 2c) was confirmed by a significant second order term in GLM, but this relied solely on the two samples with low values (at 2650 m a.s.l.

Table 1. Smoothed temperature predictor in GAM for **(A)** *Rhododendron aboreum*, **(B)** *R. aboreum* ssp. *cinnamoeum*, and **(C)** *R. aboreum* ssp. *arboreum*. $p < 0.001$ in all cases.

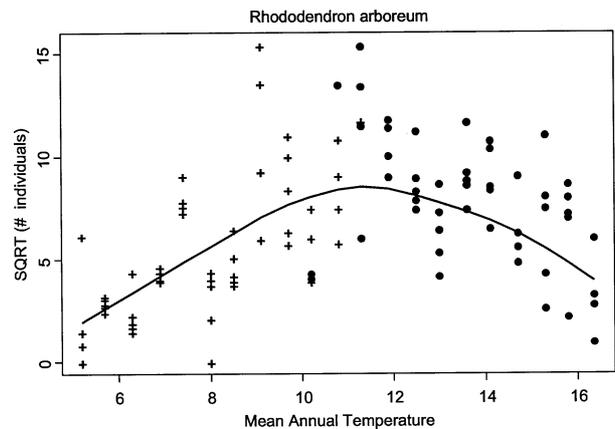|	Deviance explained	F-value	Absence values
A	39.94	17.61	Excluded
	40.72	18.50	Included
B	47.15	11.71	Excluded
	51.40	27.96	Included
C	40.41	9.87	Excluded
	66.67	52.00	Included

Fig. 1. Response model for *Rhododendron arboreum* with smoothed annual mean temperature as predictor in GAM (cf. Table 1).
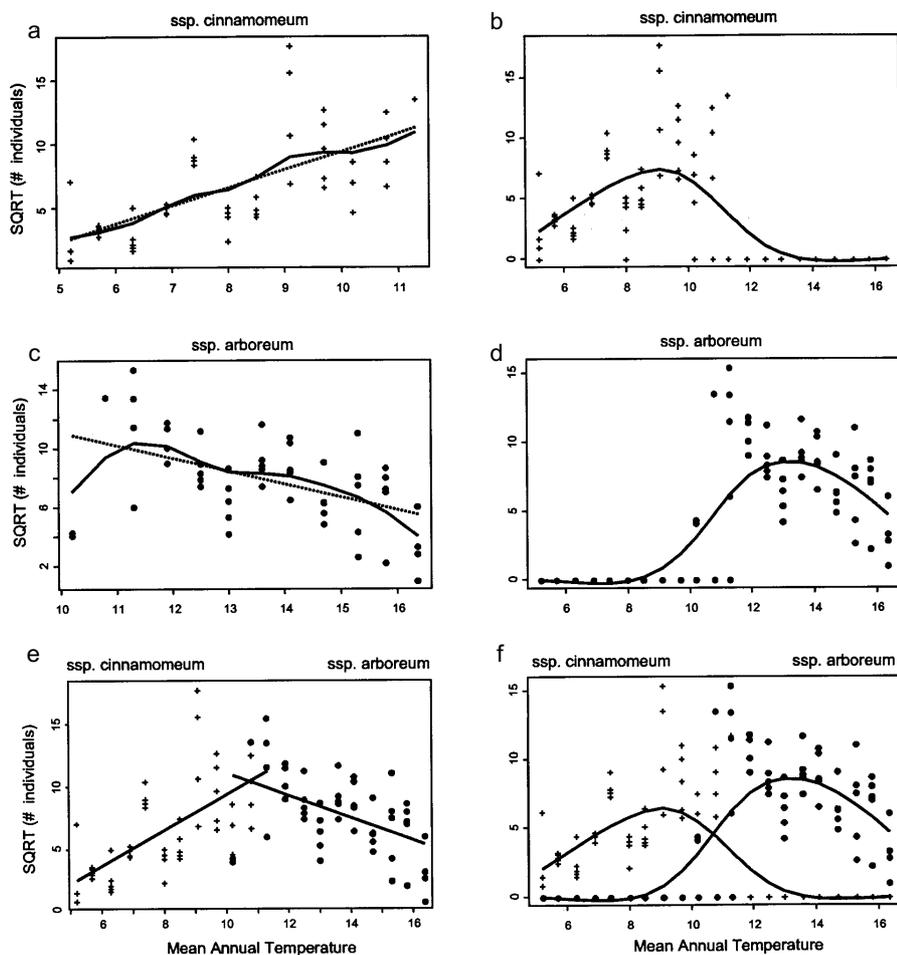
Fig. 2. GAM analyses with smoothed annual temperature as predictor and subspecies *cinnamomeum* (**a** and **b**) and *arboreum* (**c** and **d**) as responses. (**e**) is based on the combination of (**a**) and (**c**) without absence values; (**f**) is based on the combination of (**b**) and (**d**) combined with absence values (cf. Table 1). Interrupted lines (**a** and **c**) are linear models (GLM).

= 10.2 °C). However, this may be the result of a too low sampling intensity in the zone of overlap (2500-2800 m). Both subspecies have pronounced bell-shaped responses in the GAM analyses where absence values were included (Figs. 2b, d). A significant second-order polynomial in GLM confirmed this pattern.

The ambiguous niche concept (cf. Smith 1990) is to some extent clarified when the unidimensional niche is linked to the unimodal response model. Accordingly, two subspecies with distinct realized temperature niches should have a differentiated unimodal response to temperature. Although segregation in temperature was not revealed by a bimodal pattern at the species level, the two subspecies showed clear differentiation with a small overlap along the temperature gradient when analysed separately. By combining the graphs where absence values are included (Fig. 2b and 2d) two distinct temperature niches are found (Fig. 2f). The analyses without absence values, however, indicate that the subspecies do not show a proper unimodal response (Fig. 2e).

It makes sense to include plots where the target taxa do

not occur in analyses of species-environment responses as the species response curve along a given ecological variable may simply appear as the frequency distribution of that particular ecological variable if only plots where the species occur are included (Kershaw & Looney 1985: 29). A normal or skewed frequency distribution is common for environmental variables (Jongman et al. 1987), but temperature in this study is uniformly distributed.

The species *R. arboreum* has a clear unimodal response to temperature and a very long temperature range (12 °C) (Fig. 1). It is quite natural that different morphological attributes (i.e. leave indumentum) have evolved in a species which grows from the warm temperate zone up to the sub-alpine zone, which justifies the splitting of the species into two subspecies. The fact that the subspecies have distinct realized niches (if we except the inclusion of absence values), may also be used as a guide to judge the taxonomic status of the subspecies. A proper ecological niche is an important characteristics of the species concept, defined biologically (*sensu* Mayr 1982) and ecologically (*sensu* van Valen 1976; Andersson 1990). Following this rationale

one may argue that the two subspecies are actually two genuine species. Absence values in systematics, however, have a totally different meaning than in ecological analyses (cf. above). The ecological condition at the site of an individual should be regarded as a character of the individual in the same way as a morphological character. Accordingly, it does not make sense to include a character value for an individual that is not present.

In this respect the potential of the niche concept to link theory in vegetation science and systematics is not straight forward. Those who advocate an ecological species concept (van Valen 1977; Andersson 1990) should also be aware of the difficulties in defining a niche. The shape of the response curve, i.e. the niche, will depend on subjective choices by the investigator, e.g. number of plots where the target taxa do not occur. Although a niche for a taxon can be easily estimated by regression techniques, such as GLM and GAM (Austin et al. 1990, 1997; Yee & Mitchell 1991; Bio et al. 1998), the above interpretations illustrate the problems of formalizing the conceptual niche model into a more graphical or mathematical model valid within different biological disciplines. Since the results in this case depend on the numerical approach it demonstrates that the development of vegetation theory is lagging behind the rapid advances in numerical regression techniques.

References

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

Andersson, L. 1986. The driving force: species concepts and ecology. *Taxon* 39: 375-382.

Austin, M.P. 1985. Continuum concept, ordination methods, and niche theory. *Annu. Rev. Ecol. Syst.* 16: 39-61.

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., Nicholls, A.O. & Margules, C.R. 1990. Measurement of the realized qualitative niche: environmental niches of five *Eucalyptus* species. *Ecol. Monogr.* 60: 161-177.

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

Chamberlain, D.F. 1982. A revision of *Rhododendron* II. Subgenus *Hymenanthes. Notes R. Bot. Garden Edinb.* 39: 209-486.

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

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

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

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

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

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

Mayr, E. 1982. *The growth of biological thought: diversity, evolution, and inheritance.* Harvard University Press, Cambridge, MA.

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

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

Smith, R.L. 1990. *Ecology and field biology.* Harper & Row, New York, NY.

van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon* 25: 233-239.

Vetaas, O.R. & Chaudhary, R.P. 1997. Scale and species-environment relationships in central Himalayan oak forest, Nepal. *Plant Ecol.* 134: 67-76.

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.

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

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

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