Journal of Biogeography (1998) **25**, 111–122

Predicting changes in Fennoscandian vascular-plant species richness as a result of future climatic change

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Abstract. It is anticipated that future climatic warming following the currently enhanced greenhouse effect will change the distribution limits of many vascular plant species. Using annual accumulated respiration equivalents, calculated from January and July mean temperatures and total annual precipitation, simple presence–absence response surface plots are constructed for 1521 native vascular-plant species in 229 75 × 75-km grid squares within Fennoscandia. The contemporary occurrences in relation to present-day climate and to predicted changes in climate (and hence annual accumulated respiration equivalents) are used to predict possible future immigrations and extinctions within each grid square. The percentage of potential change in species richness for each grid square is estimated from these predictions. Results from this study suggest a mean increase in species richness per grid square of 26%. Increases in species richness are greatest in the southern parts of the alpine/boreal regions in Fennoscandia. There are ten species that potentially may become extinct in Fennoscandia as a result of predicted climatic warming. Possible conservation strategies to protect such endangered species are outlined.

Key words. Climate change, Fennoscandia, greenhouse effect, species richness, vascular plants.

INTRODUCTION

It is predicted that the enhanced greenhouse effect, as a result of doubled greenhouse-gas concentrations in the atmosphere, will increase mean global temperature by 3°C before the end of the next century (IPCC, 1990). Suggested increases in mean temperatures at high latitudes, including Fennoscandia, are in the range of 2–4°C for summer and 4–6°C for winter (Grammeltvedt, 1990).

Temperature is one of the most important factors controlling plant distributions at broad spatial scales (e.g. Woodward, 1987; Hengeveld, 1990; Dahl, 1992, 1998; Myklestad & Birks, 1993; Huntley *et al.*, 1995). Several studies have emphasized the thermal control of plant distributions in Norden (e.g. Iversen, 1944; Skre, 1979; Tuhkanen, 1984; Pedersen, 1990; Dahl, 1992, 1998; Myklestad, 1993). Even small changes in temperature and humidity may provoke a marked response in some species. For example, birch (*Betula pubescens*) has reacted very rapidly to temperature increases during this century in Sweden by expanding into the tundra zone (Kullman, 1983). Using predictions from general circulation models (GCMs) (IPCC, 1990), it is proposed that the boreo-nemoral zone in Fennoscandia (Norway, Sweden, Finland and Denmark) will move more than 1000 km northward from central Sweden. It has been suggested that today's *Picea*-dominated forest will be replaced by forests dominated by *Fagus*, *Quercus* and *Pinus* in the next 150–200 yr (Prentice *et al.*, 1991; Sykes, 1994; Sykes & Prentice, 1995). It can therefore be expected that major shifts in the distribution of many vascular plant species may occur during the next century in response to the predicted climate changes.

In general, a climatic warming will favour thermophilous species in Fennoscandia, whereas northern and Arctic/alpine species will potentially be threatened (Holten, 1993; Sætersdal & Birks, 1997). However, as evidence from the Holocene palaeoecological record indicates, different species show different individualistic responses (*sensu* Gleason, 1926) to a changing climate in both space and time (Huntley & Birks, 1983; Birks, 1989; Huntley, 1990; Webb, 1992). It may therefore be more appropriate to study the response of each species individually to climate change (e.g. Beerling, 1993; Elmes & Free, 1994; Beerling *et al.*, 1995) rather than to consider the response of whole vegetation types or biomes.

There are two broad approaches to the study of a species response to a possible climate warming: (1) an experimental approach, where either manipulative experiments on the effect of microclimate on the species are performed at particular sites (e.g. Mooney *et al.*, 1991; Havstrøm *et al.*, 1993), or field experiments are made to study the response of species in relation to climatic parameters such as temperature (e.g. Inouye & McGuire, 1991; MacGillivray & Grime, 1995), or (2) a correlative approach, where the distributions of particular species (e.g. Skre, 1990; Dahl, 1992, 1998; Beerling, 1993; Huntley *et al.*, 1995; Sætersdal

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& Birks, 1997) or vegetation or biome types (e.g. Emanuel *et al.*, 1985; Prentice *et al.*, 1992) are correlated to selected climatic variables of presumed physiological significance.

Several explanations for the observed correspondence between climate and plant distributions have been suggested (Carter & Prince, 1985). These explanations can be broadly divided into two:

1. Climate affects plants directly through physiological mechanisms. Different physiological mechanisms have been proposed as an explanation for different distribution patterns (Dahl, 1992, 1998). (i) Arctic/alpine plants are thought to be vulnerable to high summer temperatures (Dahl, 1951, 1992, 1998) and/or drought (Gauslaa, 1984). The physiological mechanism is thought to be protein coagulation at lethal temperatures between 43 and 53°C, which is $\approx$20°C higher than the maximum summer temperature isotherms in Fennoscandia (Dahl, 1951, 1992, 1998); (ii) oceanic species are thought to be vulnerable to damage by frost and low winter temperatures (Fægri, 1958; Lye, 1970; Skre, 1979; Dahl, 1998); (iii) it is suggested that the upper altitudinal and northern distribution limits of lowland plants may be limited by low temperatures (Dahl & Mork, 1959; Woodward & Pigott, 1975; Pigott, 1978; Skre, 1972, 1979; Dahl, 1992, 1998). Low temperatures are thought to restrict plant growth by their effects on ATP-production through dark respiration (Dahl, 1998). Different vascular plant species have different northern and/or altitudinal limits depending on how much accumulated respiration per year is required for their growth (Skre, 1979; Dahl, 1992, 1998). Annual accumulated respiration equivalents, which are the summed respiration over a year and are a measure of the potential for plant growth and ripening as a function of temperature (Dahl, 1992, 1998), can be calculated from January and July mean temperatures (Skre, 1979) as follows:

   $$\mathrm{Re} = 0.575\mathrm{T}_7 + 0.101\mathrm{T}_1 - 2.77$$

   where Re = accumulated annual respiration equivalents, T_7 = mean July temperature, and T_1 = mean January temperature. Given this equation, a 2°C increase in mean July temperature and a 4°C increase in January mean temperature following a doubled atmospheric CO_2 concentration would result in an increase in annual respiration equivalents of 1.5 units.
2. Climate affects plants indirectly, for example by modifying the habitat, including the soil (Read, 1991; Beerling & Woodward, 1994), or by changing the competitive ability of associated species (Pigott, 1978). For example the lower altitudinal limit of *Cassiope tetragona* (L.) Don, in northern Sweden, appears to be set by competition for light and nutrients (Havstrøm *et al.*, 1993).

Birks & Peglar (unpublished), using constrained ordination techniques and associated ordination diagnostics within canonical correspondence analysis (ter Braak, 1990a, 1990b), found that the present-day occurrences of 84% of the 1521 native Fennoscandian vascular plant species considered in the 229 75 × 75-km grids that comprise Fennoscandia are explained statistically by accumulated respiration equivalents better than by any other environmental variable, such as mean January or July temperatures, annual total precipitation or length of growing season. A total of eighteen environmental predictor variables (climate (eight variables), geographical (six), geological (three), land-use (one)) explain 52.5% of the variance in the 1521 species × 229 grid squares data. When used as the sole predictor variable, accumulated respiration equivalents explain 24.8% of the total variance. The environmental predictor that is strongly uncorrelated to accumulated respiration equivalents and has the highest explanatory power is total annual precipitation. When accumulated respiration equivalents and total annual precipitation are used as the only two predictors in a canonical correspondence analysis, 38.1% of the variance in the species data is explained by these two variables only. Of the eighteen environmental predictors considered, accumulated respiration equivalents and total annual precipitation explain or 'predict' the present-day occurrences better, in a statistical sense, than any other pair of predictor variables. The 1521 species considered by Birks & Peglar are all the native species with reliable distributional data for the 229 grid squares. These species represent over 90% of the total presumed native vascular-plant flora of Fennoscandia.

Accumulated respiration equivalent has a particularly strong ability to predict species distributions for a particular climate. Given temperature changes following increased greenhouse-gas concentrations in the atmosphere, the accumulated respiration equivalent isolines will change accordingly. From these, the probable change in species distribution in any area can be predicted. If this is repeated for all species in the area, and the results combined, local and regional changes in overall species richness can be predicted.

When the occurrences and/or abundances of a species are plotted along one or more macroclimatic gradients, 'bell-shaped' or Gaussian curves or responses are commonly observed (e.g. Whittaker, 1956, 1967; Austin *et al.*, 1984; Bartlein *et al.*, 1986; Hengeveld, 1990). Such responses can be modelled as a simple numerical function that describes the expected abundance of a species (the response variable) in relation to the combined effects of one or more environmental variables (the predictor variables), with each species considered independently of all others (Bartlein *et al.*, 1986). These functions are commonly non-linear and may be described by polynomials of the predictor variables (ter Braak & Looman, 1987).

The specific aims of this study are as follows:

1. To construct simple presence–absence response surface plots for the presence or absence today of all 1521 native vascular-plant species in the 229 75 × 75-km grid squares within Fennoscandia, in relation to accumulated respiration equivalents and total annual precipitation. Modelling the species' responses to climate in this way constitutes a geographical distribution analysis (*sensu* Westman, 1991), in which present-day distributions at a broad spatial scale are related to present-day climate. By

means of this analysis, the projected climate change following an enhanced greenhouse effect is used to predict changes in species distributional patterns in Norden (cf. Huntley *et al.*, 1995).

2. To use the response surface plots and predicted changes in total annual precipitation and mean January and July temperatures (and hence annual accumulated respiration equivalents) to predict the number of potential species extinctions or immigrations in each of the 229 grid squares.
3. To use these predicted floristic changes to estimate possible future patterns of regional biodiversity, to compare these predicted patterns with present-day patterns of biodiversity, and to construct maps of relative decrease or increase in regional biodiversity of vascular plants within Fennoscandia.

MATERIAL AND METHODS

The occurrences in Fennoscandia of the 1521 native plant species considered were extracted from the distribution maps in Hultén (1971). The map of Norden in Hultén (1971) was divided into 229 75 × 75-km grid squares. For each grid square the presence or absence of each species was recorded. The value of accumulated respiration equivalents for each grid was extracted from Fig. 10 in 'Naturgeografisk regioninndeling av Norden' (1977), a map of estimated annual accumulated respiration equivalent isolines. When more than one isoline occurs in the same grid square, the highest value was used. The map of annual accumulated respiration equivalents in 'Naturgeografisk regioninndeling av Norden' (1977) is based on mean monthly temperatures (1930–60) from 730 meteorological stations in Fennoscandia (O. Skre, pers. comm.). Total annual precipitation values were extracted from Fig. 9 in 'Naturgeografisk regioninndeling av Norden' (1977). For each grid square the average value was recorded and ranked from 1 to 6 according to the following scale: 1 = <500 mm/yr, 2 = 500–700 mm/year, 3 = 700–1000 mm/yr, 4 = 1000–1500 mm/yr, 5 = 1500–2000 mm/yr, 6 = 2000–2500 mm/yr.

The presence–absence response plot for present-day occurrences in relation to present-day climate was used to define the present-day climate space for *each* species (cf. Iversen, 1944). The predicted increases in January and July mean temperatures following a doubling of CO_2 according to the GCM predictions, of 4°C and 2°C, respectively, correspond to an increase in annual accumulated respiration equivalents of 1.5 units. However, in this study the annual accumulated respiration equivalents recorded from the isoline map are integers (1–9 units). We have thus used an increase in annual accumulated respiration equivalents of *only 1* unit in our predictions, i.e. we are using a conservative estimate of future change in accumulated respiration equivalents.

It has been predicted from GCMs that the increase in annual precipitation in Fennoscandia will be $\approx 10\%$. However, the change is expected to be higher in coastal (2% increase per 10 yr) than inland areas (1.5% increase per 10 yr (Sælthun, 1995)). This predicted change in annual precipitation may have little or no effect on the distribution of vascular-plant species in Fennoscandia although precipitation and humidity are important factors for some oceanic vascular-plants in Fennoscandia (Dahl, 1998). The predicted *change* in annual precipitation of 10% may thus be relatively unimportant in predicting changes in species distributions as a result of an enhanced greenhouse effect. For each grid square we have identified those species that may become extinct and the new species that may move into the grid square as a result of increased annual accumulated respiration equivalents of 1 unit. For example, a grid square with annual accumulated respiration equivalents of 7 and a total annual precipitation of 4 (1000–1500 mm/yr) today could potentially support *Phyllitis scolopendrium* (L.) Newm., given an increase in annual accumulated respiration equivalents of 1 (Fig. 1b).

We *cannot* predict changes in species richness in the southern and western parts of Fennoscandia (the Nemoral/Hemiboreal zones) because (1) some parts of western Fennoscandia with high precipitation and accumulated respiration equivalents (for example, respiration equivalents = 7 and total precipitation = 6) will experience a future climate that has no modern analogue in our study area today. Therefore, we do not know what species could thrive under such conditions. (2) For grid squares in Denmark and southern Sweden (with very high annual accumulated respiration equivalents and low annual precipitation) we do not know which species could potentially immigrate and which species will potentially become extinct because (a) the species potentially immigrating into Fennoscandia from central Europe that do not occur in Fennoscandia today have not been modelled in this study and hence we do not know what species these are, and (b) many of the species apparently becoming extinct in Denmark and southern Sweden may not do so because they also occur further south in central Europe. As we have not modelled the occurrences of these species under different climatic conditions in Germany, Poland and other areas, we do not have complete climate response plots for these species. We thus cannot comment on extinctions in southern Sweden and Denmark. Therefore, we only attempt to predict changes in species richness north of the border between the hemiboreal and the southern boreal zone (the so-called *Limes norrlandicus*) (Hustich, 1960; Ahti *et al.*, 1968).

It is possible that some species occurring to the east of Fennoscandia today may colonize eastern parts of Fennoscandia and that species apparently becoming extinct in these eastern parts will not do so, because they also occur in Russia and the Baltic States. Therefore the results from eastern Fennoscandia should be considered with some caution.

Simple presence–absence response surface plots were constructed using the program RSURF (J. M. Line & H. J. B. Birks, unpublished program), largely following the methodology of Bartlein *et al.* (1986).

Plant nomenclature follows Hultén (1971).

RESULTS

Some examples of simple presence–absence response surface plots of present-day species occurrences in relation to

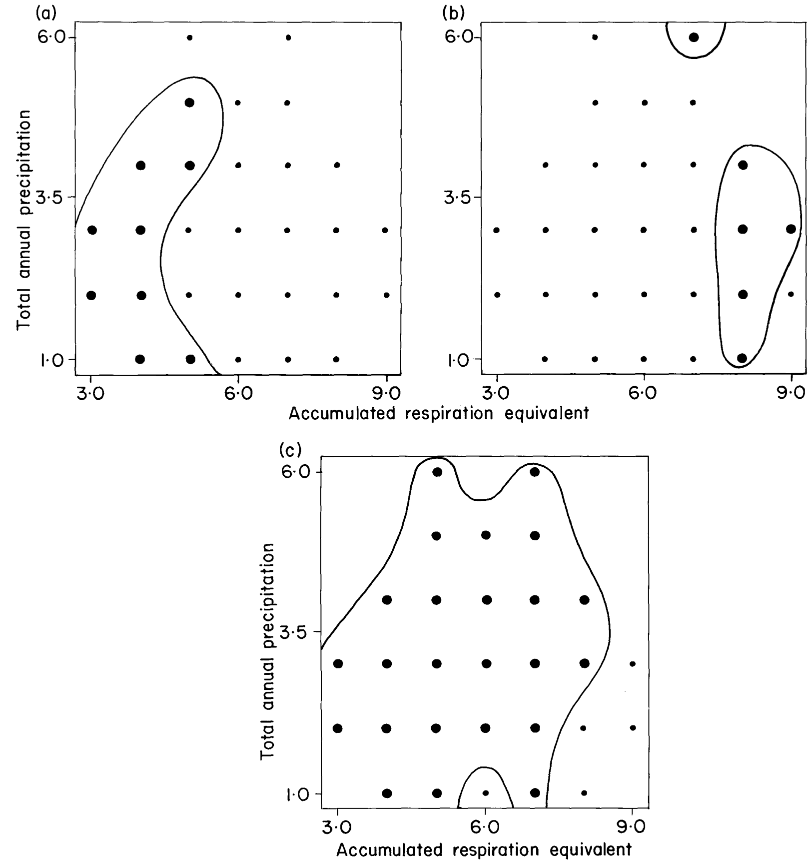

FIG. 1. Examples of simple presence–absence response surface plots of species occurrences in relation to annual accumulated respiration equivalents and annual total precipitation in Fennoscandia. (a) *Woodsia glabella*, (b) *Phyllitis scolopendrium*, (c) *Athyrium distentifolium*. Total annual precipitation is coded as 1 = <500 mm/yr, 2 = 500–700 mm/yr, 3 = 700–1000 mm/yr, 4 = 1000–1500 mm/yr, 5 = 1500–2000 mm/yr, 6 = 2000–2500 mm/yr. Large solid circles represent presence in one or more grid square, small solid circles represent absence in one or more grid square.

modern climate are shown in Fig. 1. As can be seen from these examples increased annual accumulated respiration equivalents will clearly have different effects on different species. An increase in annual accumulated respiration equivalents of 1.0 unit will cause *Woodsia glabella* R. Br., (Fig. 1a), a northern species in Fennoscandia, to move northwards and even to become extinct in some northern areas, whereas *Phyllitis scolopendrium* (Fig. 1b), a highly oceanic species in Fennoscandia, will expand its distribution into areas that currently lie beyond the modern climate space of the species. A species such as *Athyrium distentifolium* Tausch. (Fig. 1c), with a widespread distribution in Fennoscandia today, will presumably not show any major changes in its distribution.

In Fig. 2 the total number of vascular-plant species currently occurring in each grid square is shown. There is a general pattern of increased species richness as one moves from north to south.

The number of species potentially moving into each grid square, as a result of an increase in annual accumulated respiration equivalents of 1.0 unit, is shown in Fig. 3. The number of species potentially becoming extinct in each grid square as a result of increased annual accumulated respiration equivalents is given in Fig. 4. As can be seen when comparing Figs 3 and 4, the number of species potentially migrating into each grid is much greater than the loss of species as a result of potential extinctions. The difference between the percentage of potentially new species and the percentage of species potentially becoming extinct is shown in Fig. 5. This shows that potentially there may be a large increase in species number in all parts of alpine/boreal Fennoscandia. To test the null hypothesis that there is no relationship between annual accumulated respiration equivalents and predicted percentage change in species richness, a simple linear regression analysis was performed. The relationship is statistically significant ($r = 0.37$, $P < 0.01$) (Fig. 6), refuting the null hypothesis. There is thus a larger increase in species number in areas with higher annual accumulated respiration equivalents, i.e. in the southern parts of the alpine/boreal regions in Fennoscandia, than farther north.

There are ten species that potentially may become extinct in Fennoscandia as a result of an increase in annual accumulated respiration equivalents of 1.0 unit. These are: *Dryopteris fragrans* (L.) Schott, *Crepis multicaulis* Ledeb. (probably already extinct), *Braya purpurescens* (R. Br.)

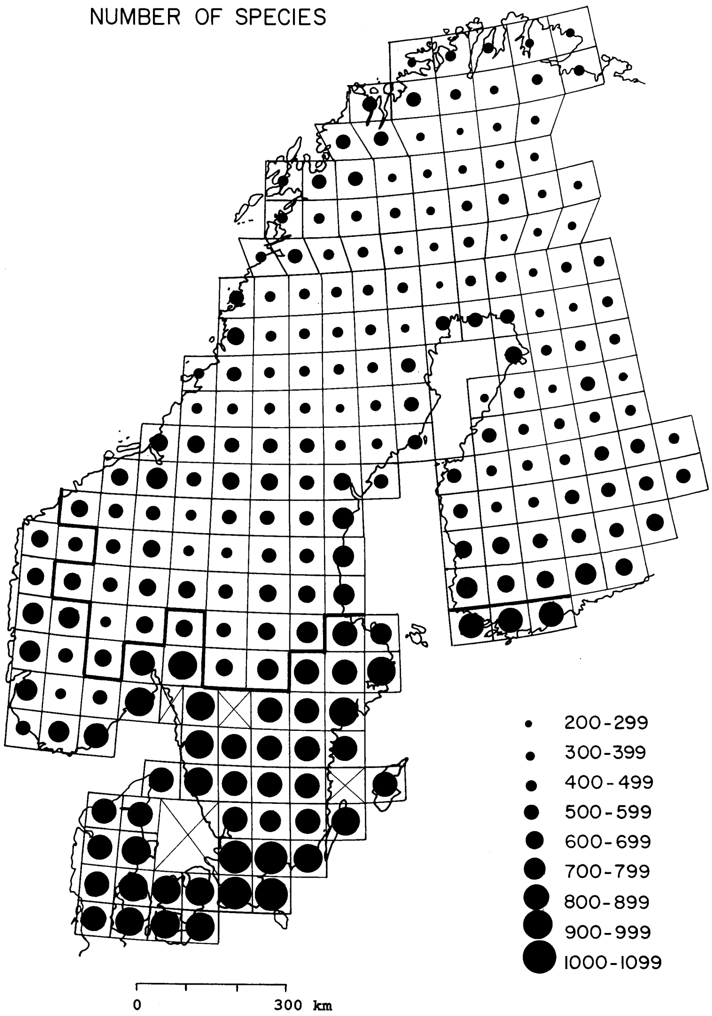

FIG. 2. The number of vascular plant species in each 75 × 75 km-grid square following the distribution maps in Hultén (1971). The thick line marks the border between the hemiboreal and southern boreal zones (the so-called *Limes norrlandicus*).

Bunge, *Carex scirpoidea* Michx., *Arctagrostis latifolia* (R. Br.) Griseb., *Oxytropis deflexa* (Pall.) Dc., *Veratrum album* L., *Papaver dahlianum* Nordh., *Polemonium boreale* Adams and *Potentilla hyparctica* Malte, all of which are restricted to northernmost Fennoscandia today. Several of these taxa are also considered by Holten & Carey (1992) to be threatened with extinction in Norway by climate warming.

DISCUSSION

The results from this study suggest a mean percentage increase in species richness per grid of 26% (Fig. 5). However, this result is based upon an increase in annual accumulated respiration equivalents of only 1 unit, i.e. a conservative estimate of the projected climatic change during the next 50 yr suggested by the GCM models (e.g. Hansen *et al.*, 1984, 1988; Washington & Meehl, 1989; IPCC, 1990). Even this moderate climate change may result in a considerable change in richness of vascular-plants within the boreal and alpine regions in Fennoscandia (Figs 5 and 6). It can be expected that if the GCM prediction results are correct, the potential change in species richness may be even more dramatic than the results from this study indicate.

The method used in this study, relating present-day distributions with present-day climate so as to predict future distributions, is useful in predicting the magnitude of potential changes in species richness patterns. However, as pointed out by Malanson (1993), such correlative methods do not take into account the fact that species need to disperse to new areas as climate changes. In correlative methods, it is assumed that the dispersal abilities of all species are equal and that dispersal mechanisms are not important in determining species distribution patterns (e.g. Sykes & Prentice, 1995; Huntley *et al.*, 1995). Our results should therefore be interpreted with some caution. Although dispersal may be an important factor in influencing the ranges of some species, we believe that the general prediction of increasing species richness as a result of increasing temperature found in this study is realistic.

Little is known about the dispersal abilities and rates of spread of vascular-plant species. In order to track a rapid climate warming, species will have to disperse northwards

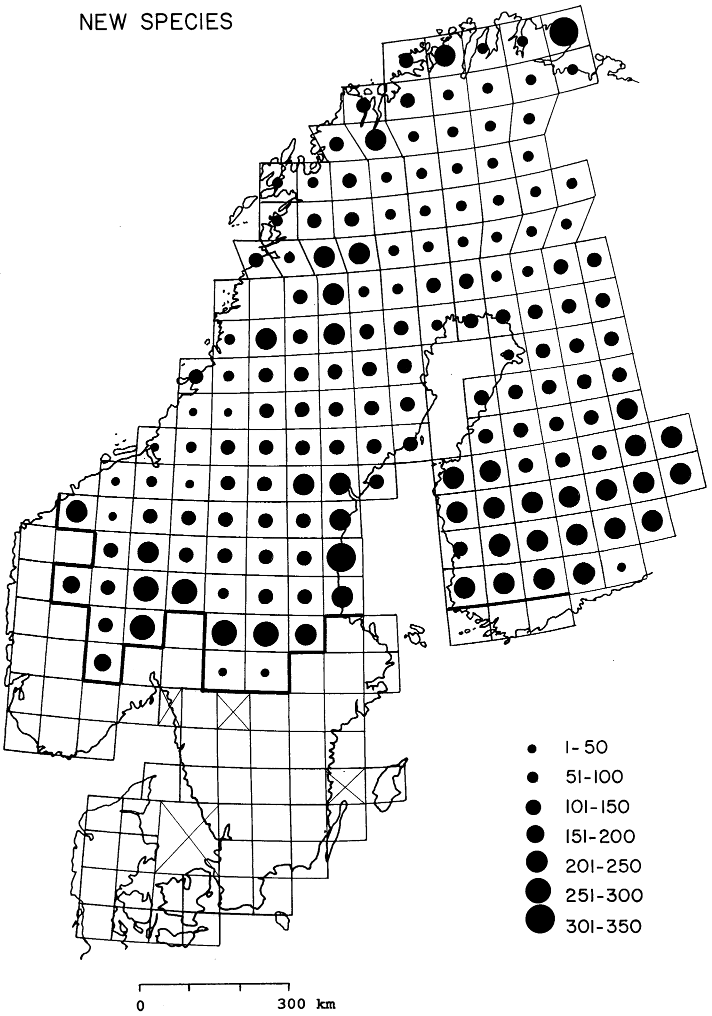

FIG. 3. The potential number of new species immigrating into each grid square as predicted by a change in annual accumulated respiration equivalents (1 unit) following an enhanced greenhouse effect. Blank grids mean that no predictions about changes in species richness are possible.

or to higher elevations. There are, however, two major types of dispersal limitations that may influence the dispersal abilities of plant species: (1) intrinsic limitations to dispersal; these include ecological characteristics, such as fecundity, dispersal mechanism, tolerance of selfing and inbreeding, competitive ability, and ecotype differentiation (Peters, 1991; Holten, 1993); and (2) extrinsic barriers to dispersal. These include physical barriers such as oceans, lakes, mountains, agricultural areas, urban areas, clear-felled areas and edaphic or other habitat barriers. The latter may be particularly important for calcicolous or other edaphically demanding species (Boer *et al.*, 1990; Holten, 1993). The problem of extrinsic barriers in the boreal and alpine regions of Fennoscandia seems to be less than in continental Europe for several reasons. First, human-caused habitat destruction, for example the heavily cultivated continental European plains, is not as extensive in Fennoscandia as in the rest of Europe. Second, a large change in latitude in Fennoscandia corresponds to a small change in altitude. For example, a 3°C warming leads to a climatic shift of ≈250 km in latitude, corresponding to approximately only 500 m in elevation (MacArthur, 1972; Nimis, 1984a, 1984b). This suggests that in mountainous areas species may have a better chance of tracking future climate change. In Fennoscandia, the Scandinavian mountain chain runs north–south from southern Norway along the Norwegian/Swedish border until the very north of Fennoscandia. This is a situation similar to that of the North American mountain chains, which also run north–south. North America experienced fewer plant extinctions during the Pleistocene glacial/interglacial cycles than in Europe, possibly because the North American mountain chains were not barriers to the south- or northward movement of species, in contrast to the central European mountain chains which run west–east (van der Hammen *et al.*, 1971; Tralau, 1973; cf. Currie & Paquin, 1987; Huntley, 1993). By migrating upwards in altitude, the north–south orientation of the Scandinavian mountain chains may provide a quicker route to climatically cool refuges than a long migration northwards.

Several authors (e.g. Roberts, 1989; Peters, 1991;

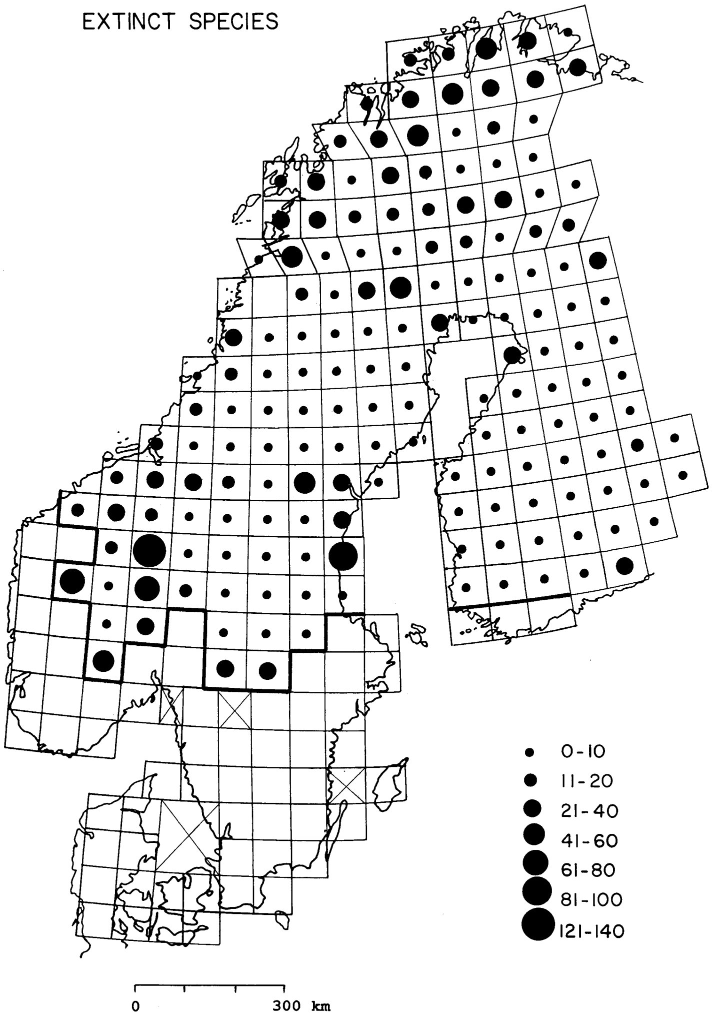

FIG. 4. The potential number of species going extinct in each grid square as predicted by a change in annual accumulated respiration equivalents (1 unit) following an enhanced greenhouse effect. Blank grids mean that no predictions about changes in species richness are possible.

Schneider *et al.*, 1992) have suggested that climatic change over the next 50 yr could be 10–40 times faster than the average rate of warming following the last glaciation. However, recent evidence from Greenland ice-cores suggests that the transitions between cold and temperate stages during the late Pleistocene are characterized by abrupt fluctuations in climate that may have occurred over periods of less than 20 yr (Taylor *et al.*, 1993). If this is correct, the expected climate warming will *not* occur at a rate several times faster than natural variations in climate. Hence, the expected climate warming over the next 50–100 yr will not necessarily have more severe consequences than the change to temperate conditions at the end of the last glaciation. However, when temperature increased at the end of the last glaciation regional or local extinctions of vascular plants occurred. For example, *Papaver* sect. *Scapiflora* seems to have been widespread beyond the ice-sheet margins in Fennoscandia and in the British Isles during the late-glacial period, but it is now restricted to a few mountain localities in Fennoscandia (Birks, 1994). *Magnolia*, *Tsuga* and *Thuja* experienced complete extinctions from Europe during the Pleistocene (Tralau, 1973).

The predicted increase in species richness in Fennoscandia (Fig. 5) can only be reached if a new climatic equilibrium, such as occurred in the late Holocene (Nesje, 1992), takes place. If, as is possible, the temperature continues to increase after $2 \times CO_2$ levels are reached the consequences on biodiversity in Fennoscandia may be even more drastic than suggested by this study.

A predicted increase in species richness following increased temperature (Fig. 5) is not surprising. One of the most striking patterns in biogeography is that of increasing species richness from the Arctic to the tropics (Pianka, 1966; Stevens, 1989). Although there are some exceptions to this pattern (e.g. Järvinen & Väisänen, 1978; Myklestad & Birks, 1993), most organisms show a clear latitudinal decrease in richness from south to north (e.g. McCoy & Connor, 1980; Stevens, 1989; Pagel *et al.*, 1991). This decrease also occurs with increasing altitude (Stevens, 1992). Several explanations have been proposed to explain this pattern

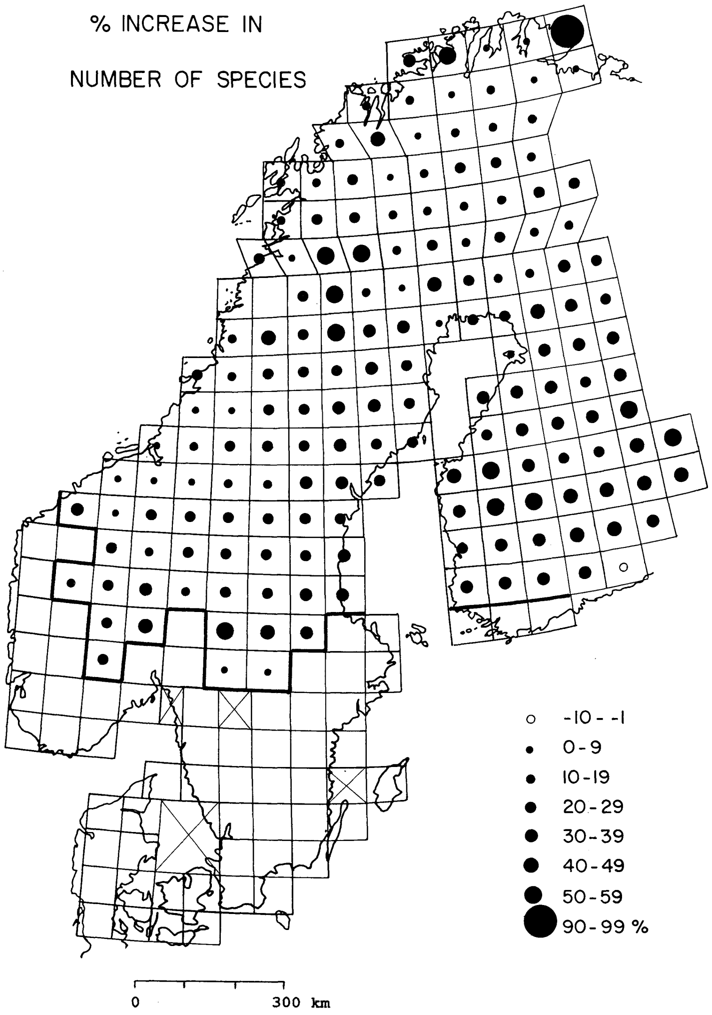

FIG. 5. Percentage change in species richness in each grid square as predicted by a change in annual accumulated respiration equivalents (1 unit) following an enhanced greenhouse effect. Blank grids mean that no predictions about changes in species richness are possible.

(e.g. Pianka, 1966). The species–energy theory (Brown, 1981; Wright, 1983), which proposes that the species number in any area is limited by the quantity of energy available in the area, is supported by evidence for plants at different spatial scales (Wright, 1983; Currie & Paquin, 1987; Moore & Keddy, 1989; Adams & Woodward, 1989; Currie, 1991; cf. Latham & Ricklefs, 1993).

In our predictions there are extreme increases in species number in some grid squares (e.g. grid no. 5 in the far north east, with an increase in species richness of 98%) (Fig. 5). This extreme increase is probably due to an incomplete knowledge of the flora in that grid square today. Under-recording may also be a problem in some other grid squares, especially in remote areas. However, we feel that the distribution maps used in this study (Hultén, 1971) are generally adequate and appropriate for the mapping of broad-scale patterns of species occurrences and richness in Fennoscandia.

Figure 6 shows that the percentage of increasing species richness is positively correlated with the annual accumulated respiration equivalent. A possible explanation for this is that grid squares with the highest annual accumulated respiration equivalents are situated at the transition (*Limes norrlandicus*) between the boreal and hemiboreal zones. The hemiboreal zone is characterized by a mixture of boreal species and nemoral species, such as *Tilia cordata* Mill., *Quercus robur* L., *Ulmus glabra* Huds. and *Corylus avellana* L. (Hustich, 1960). These species and other associated broadleaved deciduous woodland species constitute a totally new set of species in the present boreal zone (the new hemiboreal zone). However, many of these species require brown-earth soils for establishment, and it is therefore expected that species such as these with specific edaphic demands may show a considerable time-lag in their spread and establishment, due to the time it takes for podsols to be transformed into brown-earth soils, before they are able to establish themselves (Holten & Carey, 1992).

From a species conservation perspective the potential increase in species number *per se* is unproblematic. However, an increased species richness is certainly problematic if, for example, rare Arctic or Arctic/alpine species become extinct because of a warming climate and/or competition from

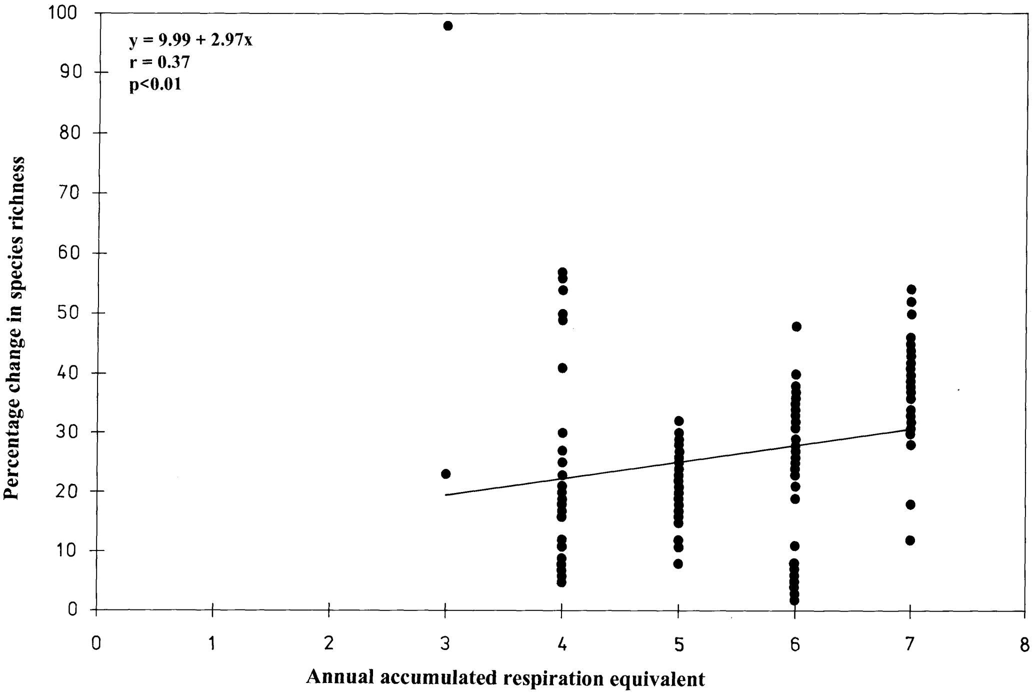

FIG. 6. The relationship between annual accumulated respiration equivalents and predicted percentage change in species richness for the grids mapped in Figs 3, 4 and 5.

expanding southern species (Sætersdal & Birks, 1997). The predictions from this study suggest that at least ten northern or Arctic species are potentially threatened by extinction as a result of an increase in annual accumulated respiration equivalents of 1 unit (cf. Holten & Carey, 1992).

The predicted rapid climate change makes it even more difficult for conservationists today to select the most appropriate nature reserves for the future (Pressey *et al.*, 1993; Sætersdal & Birks, 1993; Sætersdal *et al.*, 1993). As species or communities of interest are predicted to move northwards or upwards, the selection of nature reserves may become similar to trying to shoot at a moving target! One important strategy to minimize extinctions is to preserve, now, more than simply the minimum. As emphasized by Peters (1991, 1992), the less populations are reduced at the present day, the more resilient they will be to climatic change in the future. This implies that we urgently need more and larger reserves. This will also maximize the probability of small patches with the right microclimate being preserved. The new reserves should be designed to minimize the loss of species due to climate change. First, the reserves should encompass as much altitudinal variation as possible. Second, they should be located near the northern/upper distribution limit today of species or communities of conservation concern (Peters, 1991). However, for some species, such as mountain plants, there may be nowhere for them to migrate to because they are already at the top of the mountains. For these species the only viable conservation policy may be to transplant them to other mountain areas where the climate is predicted not to become too warm in the future, for example on mountains further north or at higher altitudes. Clearly such transplants must be carefully designed and documented and should only be attempted when no other conservation stategy appears possible or effective.

In conclusion, the predicted climate warming may potentially give dramatic changes in regional species richness in boreal/alpine parts of Fennoscandia. Careful management strategies are needed, however, to protect endangered species from local and even regional extinction.

ACKNOWLEDGMENTS

We are grateful to John M. Line for programming RSURF and for helpful discussions, Hilary Birks, the late Eilif Dahl, Klaus Høiland, and Des Thompson for valuable discussions, Åse Myklestad for critically reading the manuscript, and an anonymous reviewer for valuable comments. Financial support was received from NAVF/NFR (grants no. 456.90/017 and 454.88/001) and Sogn & Fjordane College.

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