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*Natural mixed forests of European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*), and silver fir (*Abies alba*) were widely replaced by spruce-dominated stands in the montane belt of the northern Calcareous Alps in historical times. This accounts for changing forest structure, diversity, and hemeroby. Observations in other parts of Europe suggest that this development should have led to a replacement of the native understorey vegetation by species typical of coniferous forests and to an increase in plants that are indicators for acidity and nitrogen. The statistical relationships between understorey vegetation structure and species richness, Ellenberg indicator values, and the proportion of Norway spruce in the tree layer were studied in 84 stands selected in a stratified random design in the Bavarian Alps, while controlling for the influence of the natural environment. The results show that the richness of coniferous forest species and the occurrence of acid indicators have been significantly favored by Norway spruce canopies, while understorey species characteristic of deciduous forests and nitrogen indicators have not been affected. While bryophytes and some shallow-rooted vascular plants respond positively to a coniferous canopy, most vascular plants are resilient to changes in the canopy. This can be attributed to the high buffering capacity of the soils under the mountain forests studied.*

Introduction

The degree to which vegetation has been altered by human intervention is becoming more important in rating the conservation value of forest resources throughout the developed countries of the Northern Hemisphere (Franklin 1988; Seymour and Hunter 1999). Thus, based on the concepts of Jalas (1955) and Blume and Sukopp (1976), the hemeroby (ie, the reciprocal of naturalness) of forests in Austria was recently assessed in a Man and the Biosphere project (Grabherr et al 1998). Anthropogenic changes in tree layer species composition are regarded as a key attribute of hemeroby, ranking above understorey composition and diversity. In fact, changes in canopy dominance are likely to

have impacts on many ecosystem properties, such as the diversity of the entire biotic community and soil quality. However plausible these impacts may be, scientific evidence for them is not easy to obtain because tree species impacts are longterm and often confounded by differences in primary ecological factors (Ulrich et al 1971; Binkley 1995).

If man-made changes in tree species composition alter understorey composition, the use of indicator plants (Ellenberg et al 1991) and character species (Braun-Blanquet 1964; Oberdorfer 1994) in the mapping of potential natural vegetation may be severely hindered. This is of particular relevance in the Alps, where vegetation is widely used in forest site classification (Schmider and Burnand 1988; Frey 1995; Ewald 1999).

At the northern fringe of the Alps, montane forests ranging from 600 to 1400 m were composed of European beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* [L.] Karst.), and silver fir (*Abies alba* Mill.) prior to human interference (Zukrigl 1973; Ewald 1997; Keller et al 1998). Palynological and historical records indicate that, in many parts of the northern Alps, tree species composition was altered in favor of Norway spruce in historical times (von Bülow 1962; Kral 1979; Burga and Perret 1998). Meister (1969) identified selective browsing by deer that increased in density due to game preservation, forest pasturing, clear-cutting, artificial seeding, and planting as the causal agents behind this secular process. Such a change in canopy composition alters the living conditions of understorey plants, as mixed forests are replaced by pure conifer stands. Instead of nutrient-rich deciduous litter, spruce needles rich in polyphenols come to dominate the physical and chemical properties of the forest floor (Wittich 1961). Furthermore, coniferous canopies with their higher leaf area index and evergreen foliage filter larger amounts of atmogenic acids from the air (van Breemen et al 1983; Kreutzer et al 1986). The conversion to Norway spruce is therefore likely to speed up soil acidification and induce the accumulation of poorly digested forest floor material, as Nihlgard (1971) showed in southern Swedish plantations. As a result, native understorey species with high demands on nutrients may decline in favor of acidophilous vegetation (Nihlgard 1970). The same effect was found in the foreland of the Swiss Alps (Teuscher 1985). Ewald (1997) hypothesized that spruce dominance favors character species of coniferous forests, which entails a danger of incorrect classification of potential natural vegetation. Recent studies in the Black Forest (Bürger 1991) and in northern Germany (Lücke and Schmidt 1997) indicate that artificial spruce stands have been subjected to a particularly rapid immigration of indicators of eutrophication due to elevated atmospheric nitrogen inputs.

TABLE 1 List of the variables measured in the study.

	Defined as	Measured by
Dependent variables		
Understorey sample	12 × 12-m quadrat	Visual
CoQFAll	Cumulative cover of *Querco-Fagetea* species	Sum
CoVPAll	Cumulative cover of *Vaccinio-Piceetea* species	Sum
CoQFVasc	Cumulative cover of vascular *Querco-Fagetea* species	Sum
CoVPVasc	Cumulative cover of vascular *Vaccinio-Piceetea* species	Sum
CoveVasc	Horizontal cover of vascular field layer	Visual
CoveBryo	Horizontal cover of bryophyte layer	Visual
CoveTReg	Cumulative cover of tree regeneration in understorey	Sum
RiQFAll	Number of *Querco-Fagetea* species	Count
RiVPAll	Number of *Vaccinio-Piceetea* species	Count
RiQFVasc	Number of vascular *Querco-Fagetea* species	Count
RiVPVasc	Number of vascular *Vaccinio-Piceetea* species	Count
TotRich	Total number of species in understorey	Count
RichVasc	Number of vascular plant species	Count
RichBryo	Number of bryophyte species	Count
RichTReg	Number of tree species in understorey	Count
mRall	Ellenberg indicator value for soil reaction (all species)	Mean
mRvasc	mR (vascular species only)	Mean
mN	Mean Ellenberg indicator value for nitrogen	Mean
Explaining variable		
Tree layer composition	Woody perennials >5 m in 24 × 24-m quadrat	Visual
PropPice	Proportion of Norway spruce cover in tree layer (%)	Calculation
Covariables	Attributes considered independent of tree layer	
mMinSoil	Mineral soil depth (median of four measurements) (cm)	4 augerings
mDecarbo	Depth of free carbonate from mineral soil surface (median) (cm)	4 augerings, HCl probe
mMottlin	Depth of visible hydromorphic mottles (median) (cm)	4 augerings
Elevat	Elevation asl (m)	Barometric
Aspect	Favorability index: $\cos(aspect_{max} - aspect) + 1$ with aspect in degrees and $Aspect_{max} = 202.5°$ (0; 2)	Compass
Inclinat	Slope inclination (°)	Inclinometer
TLCumCov	Horizontal area shaded by tree layer (%)	Visual estimation

Examining a representative sample of forest vegetation offers the chance to investigate which changes in species composition occurred in the montane belt of the Bavarian Alps. The present study aims to test hypotheses that tree stands with currently high proportions of Norway spruce could possess (1) fewer character species of temperate deciduous forests, (2) more character species of boreal/subalpine coniferous forests, (3) more plant indicators of acid conditions, and (4) more indicators of high nitrogen supply than mixed coniferous-deciduous and pure deciduous stands at comparable sites.

TABLE 2 Character species of deciduous forest (*Querco-Fagetea*) and of coniferous forest (*Vaccinio-Piceetea*) and their occurrence (% constancy) and mean dominance (% cover) in the mountain forests studied; M designates bryophytes.

Character species	Deciduous forest *Querco-Fagetea*		Character species	Deciduous forest *Querco-Fagetea*	
	Occurrence (% constancy)	Dominance (% cover)		Occurrence (% constancy)	Dominance (% cover)
Mercurialis perennis	70	6.5	*Polystichum lobatum*	14	0.9
Sanicula europaea	67	2.4	*Cardamine trifolia*	13	3.4
Viola reichenbachiana	65	1.2	*Impatiens noli-tangere*	13	1.8
Brachypodium sylvaticum	61	4.3	*Anemone nemorosa*	12	1.3
Carex sylvatica	58	1.2	*Cardamine flexuosa*	12	0.5
Carex digitata	57	1.3	*Bromus ramosus* ssp. *Benekenii*	10	0.5
Phyteuma spicatum	52	1.1	*Circaea alpina*	10	1.1
Veronica urticifolia	52	0.6	*Aconitum vulparia*	8	0.5
Lysimachia nemorum	51	1.3	*Actaea spicata*	8	1.2
Galium odoratum	49	2.6	*Stachys sylvatica*	8	0.9
Lamiastrum montanum	45	1.4	*Circaea lutetiana*	7	1.3
Hepatica nobilis	40	2.0	*Adoxa moschatellina*	6	0.5
Melica nutans	40	1.4	*Aruncus dioicus*	6	1.0
Daphne mezereum	39	0.5	*Campanula trachelium*	6	0.5
Hordelymus europaeus	39	1.1	*Chrysosplenium alternifolium*	6	0.5
Plagiomnium undulatum M	35	3.2	*Myosotis sylvatica*	6	0.5
Primula elatior	35	0.7	*Circaea x intermedia*	5	1.8
Salvia glutinosa	35	1.7	*Convallaria majalis*	5	1.1
Aposeris foetida	33	1.5	*Festuca gigantea*	5	1.1
Paris quadrifolia	32	0.6	*Poa nemoralis*	5	0.5
Petasites albus	31	6.1	*Clematis vitalba*	4	0.5
Dryopteris filix-mas	30	1.2	*Hedera helix*	4	0.5
Sorbus aria	29	1.0	*Cephalanthera rubra*	2	0.5
Ajuga reptans	27	1.2	*Eurhynchium swartzii* M	2	0.5
Fissidens taxifolius M	27	0.7	*Pulmonaria officinalis*	2	1.8
Epilobium montanum	19	0.5	*Allium ursinum*	1	10.0
Veronica montana	18	1.2	*Asarum europaeum*	1	3.0
Epipactis helleborine	15	0.5	*Cardamine impatiens*	1	0.5
Lilium martagon	15	0.5	*Milium effusum*	1	0.5
Lonicera alpigena	15	0.9	*Scrophularia nodosa*	1	0.5
Neottia nidus-avise	15	0.5			
Ranunculus lanuginosus	15	1.8			
Lonicera xylosteum	14	0.7			

In order to remove the influence of site conditions that vary independent of the dominant tree species, the influence of environmental covariables was controlled in a partial correlation analysis (Legendre and Legendre 1998). This statistical method allows isolation of the ecological effect of canopy species across the wide range of environments present in a complex mountain landscape and prevents misinterpretations resulting from the non-random distribution of stand types across site types.

Material and methods

The vegetation sample was drawn from a monitoring network (Ewald and Reuther 1999) situated in the

Character species		Coniferous forest *Vaccinio-Piceetea*	
		Occurrence (% constancy)	Dominance (% cover)
Vaccinium myrtillus		52	2.5
Luzula sylvatica ssp. *Sieberi*	M	35	6.7
Rhytidiadelphus loreus		35	2.3
Huperzia selago		31	0.5
Homogyne alpina	M	30	1.0
Bazzania trilobata	M	24	0.6
Pleurozium schreberi		24	2.2
Lycopodium annotinum	M	20	3.9
Calypogeia azurea	M	14	0.5
Mylia taylori	M	14	1.1
Plagiothecium undulatum		14	0.9
Blechnum spicant	M	11	0.8
Hylocomium umbratum		11	2.4
Lonicera nigra		10	0.8
Luzula luzulina	M	8	0.5
Ptilium crista-castrensis		7	2.9
Clematis alpina	M	6	1.5
Barbilophozia lycopodioides		4	0.5
Calamagrostis villosa		4	4.5
Vaccinium vitis-idaea		4	1.3
Listera cordata	M	2	0.5
Calypogeia neesiana		1	0.5
Pinus mugo		1	3.0
Rhododendron hirsutum		1	0.5
Sorbus chamae-mespilus		1	0.5

northern Calcareous Alps near Garmisch-Partenkirchen, Germany (11°4'–11°10'E, 47°24'–47°36'N). The montane forests studied occur between elevations of 630 and 1400 m, above which they are replaced by subalpine Norway spruce and dwarf pine (*Pinus mugo* Turra). Climate is cool montane (mean annual temperatures of 4–7°C, precipitation 1400–ca 2000 mm; Fliri 1975). Geo-

logical parent materials are diverse and give rise to a wide variety of soil types. Limestones/dolomites favor rendzina-type shallow soils rich in carbonates (Rendzic Leptosols according to FAO-UNESCO 1997), mudstones/schists develop into clayey and often waterlogged deep soils (Eutric Cambisols and Gleysols), and sandstones/siliceous limestones give rise to sandy acid soils (Eutric to Dystic Cambisols, rarely Podsols). Historically, pasturing and logging have been well documented since the 14th century. Early settlements can even be traced back to Roman times (Hauke 1988). Since the 19th century, preserving and winter feeding have resulted in high populations of red deer (*Cervus elaphus*), which are regarded as the main cause of a widespread decline of mixed forest in favor of Norway spruce (Figure 1). As silver fir has suffered most from this development, present-day stand types vary mostly from pure spruce to spruce-beech and occasional pure beech.

The selection of sampling points was based on an extensive forest inventory (see Ewald and Reuther [1999] for details) that allowed for preselection of stands older than 60 years and for stratification into stand types (pure spruce, mixed, pure beech), soil groups (6 classes), altitudinal zones (below and above 1000 m), slope aspect (sun-exposed, shaded), and petrography (5 zones read from a geological map). Sample points were drawn at random from 84 strata, thus providing a balanced sample, in which intercorrelations between stratification criteria are minimized.

At each sampling point, the variables listed in Table 1 were recorded. The first group describes diversity, composition, and structure of understorey vegetation types that served as dependent variables in statistical analysis. The classification of species into groups of deciduous forest (*Querco-Fagetea*) and coniferous forest (*Vaccinio-Piceetea*) was taken from the supraregional phytosociological study by Ewald (1997, Table 2). The number of species belonging to sociological groups was counted and cover values were summed per plot, once for all species and once for vascular plant species only. Understorey richness was calculated for all species and for vascular plants, bryophytes (mosses and liverworts), and tree regeneration (seedlings and saplings) separately. Total cover of vascular field layer and bryophyte layer were estimated visually in the field. Indicator values were taken from the list of Ellenberg et al (1991) and calculated as the simple mean of all species occurring in each 144-m^2 understorey sampling plot. Ellenberg's indicator value R expresses the ecological preference of plant species for soil pH on an ordinal scale from 1 to 9. Similarly, Ellenberg's N arranges plants with respect to their preference for varying levels of nitrogen availability. The arithmetic mean, mR, was calculated both with and without inclusion of bryophytes.

a

b

The explaining variable describing the proportion of spruce cover in the canopy (*PropPice*) was calculated as the percentage of *Picea* cover in the cover sum of all tree species recorded on a 24 × 24-m plot comprising the understorey sample at its center. Depth of mineral soil development and free carbonate were used as covariables since these soil properties—contrary to the dependent topsoil attributes—are not likely to be influenced by changes of canopy composition. They thus represent the component of water-retention capacity and trophic level that does not depend on the present state of the ecosystem. To account for the edaphic variability typical of mountain environments, soil profiles were inspected in 4 replicate augerings at 4 m from the plot center, and plot medians were used in statistical analysis. Slope exposition was transformed from angles to a favorability index (Beers et al 1966) by defining 157.5° as the most favorable thermal aspect. The total horizontal cover of the tree layer was included as a covariable to remove differences in stand management (thinning) that tend to reduce canopy density of Norway spruce stands in accessible locations.

Partial correlation analysis was carried out with SPSS for WINDOWS 9.0.1 software. *PropPice* was related to individual dependent variables while controlling for any linear effect of covariables. Partial correlation coefficients were tested for two-tailed significance.

Results

Besides giving an account of partial correlations and their significance (Table 3), this section shows the interplay between covariables and canopy composition in controlling vegetation attributes (Figures 2–4). The covariables with the highest simple correlation with the study variable of interest were selected for these scatterplots.

Of the 7 understorey cover variables (Table 3), only the bryophyte layer (*CoveBryo*) showed a significant pos-

itive partial response to the proportion of Norway spruce in the canopy (*PropPice*). Figure 2 shows that bryophyte cover increases both under spruce canopy and on flatter slopes. The significant partial relationship is due to the fact that high bryophyte cover on steep slopes was only encountered in stands dominated by spruce. Among the species-richness variables, the coniferous forest (*Vaccinio-Piceetea*) species with and without bryophytes and bryophyte richness respond positively to the partial influence of spruce canopy. Apart from being influenced by the canopy, bryophyte richness is most closely related to elevation (Figure 3).

The mean indicator value for soil reaction exhibits a negative partial relationship with *PropPice,* which becomes less pronounced when bryophytes are omitted. It can be read from Figure 4 that the differences in *mR* between deciduous and coniferous stands occur on soils with intermediate and great depths of free carbonate, whereas the occurrence of acid indicators on soils rich in carbonate was not related to canopy composition. There is no significant relationship between the indicator value for nitrogen and canopy composition. The negative correlation coefficient indicates that *mN* tends to be somewhat lower in stands dominated by spruce.

Conclusions and discussion

The significant partial effects of Norway spruce on vegetation suggest that hypotheses 2 and 3 hold up in the Bavarian Alps. Coniferous forest species and indicators of acidity occur in greater numbers in spruce stands than in mixed and deciduous stands at comparable sites. Lower pH in the uppermost humus layers may be ascribed to the higher release of organic acids from decomposing needle litter and, possibly, to higher atmogenic inputs of acids by canopy filtering (Ewald 2000). Contrary to expectations, the richness and abundance of deciduous forest species and the indicator values for nitrogen varied independently of canopy composition, so hypotheses 1 and 4 must be rejected.

The most pronounced effect on vegetation, which is not restricted to species richness but also has an effect on dominance structure, is on bryophytes. Bryophytes are clearly more abundant and more diverse in the presence of spruce. This corresponds to the findings of Lücke and Schmidt (1997) on artificial plantations in the Solling forest (northern Germany). Experiments by Longton and Greene (1979) showed that growth of the moss *Pleurozium schreberi* (Brid.) Mitt. was

Dependent variable	Partial correlation	Significance	Simple rank correlation	Covariable (with highest simple correlation)
CoQFAll	-0.0375	0.746	NS -0.050	Aspect (*-0.275)
CoVPAll	0.1259	0.275	***0.386	TLCumCov (***-0.370)
CoQFVasc	-0.0396	0.733	NS -0.082	Aspect (*-0.257)
CoVPVasc	0.0374	0.747	NS 0.198	Elev. (***0.336)
CoveVasc	0.1557	0.176	***0.398	TLCumCov. (***-0.566)
CoveBryo	***0.4286	0.000	***0.689	TLCumCov. (***-0.439)
CoveTReg	-0.1440	0.324	NS -0.148	Elev. (***-0.517)
RiQFAll	-0.1879	0.102	NS -0.170	MMinSoil (NS 0.170)
RiVPAll	**0.3236	0.004	***0.429	TLCumCov. (***-0.405)
RiQFVasc	-0.2099	0.067	NS -0.180	MMinSoil (NS 0.128)
RiVPVasc	*0.2330	0.041	*0.253	Elev. (***0.431)
RichAll	0.1577	0.171	**0.327	TLCumCov. (***-0.453)
RichVasc	0.0190	0.870	**0.293	TLCumCov. (***-0.481)
RichBryo	***0.4297	0.000	***0.398	Elev. (***0.342)
RichTReg	-0.0789	0.495	NS -0.021	Elev. (***-0.647)
mRAll	**-0.3476	0.002	**-0.315	mDecarbo (***-0.513)
mRVasc	*-0.2672	0.019	NS -0.202	mDecarbo (***-0.563)
mN	-0.2227	0.052	*-0.225	mMinSoil (***0.638)

TABLE 3 Partial correlation coefficients between proportion of spruce in canopy and dependent variables; NS: not significant, *: p<0.05, **: p<0.01, ***: p<0.001.

inhibited by the shading effect of broad-leaved litter. This suggests that the slow-growing bryophytes are simply relieved from inhibition by beech litter in coniferous stands. The vascular *Vaccinio-Piceetea* species are more numerous but not more dominant in spruce
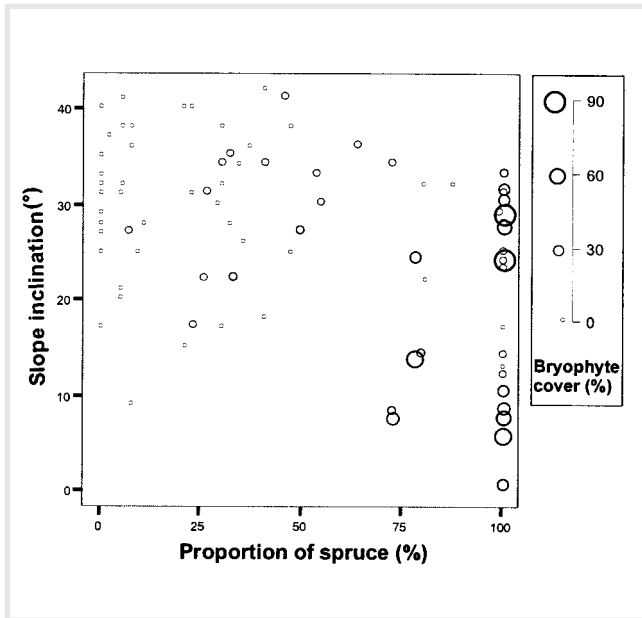

FIGURE 2 Scatterplot showing the proportion of Norway spruce at various slope inclinations, with bryophyte cover depicted as circles.
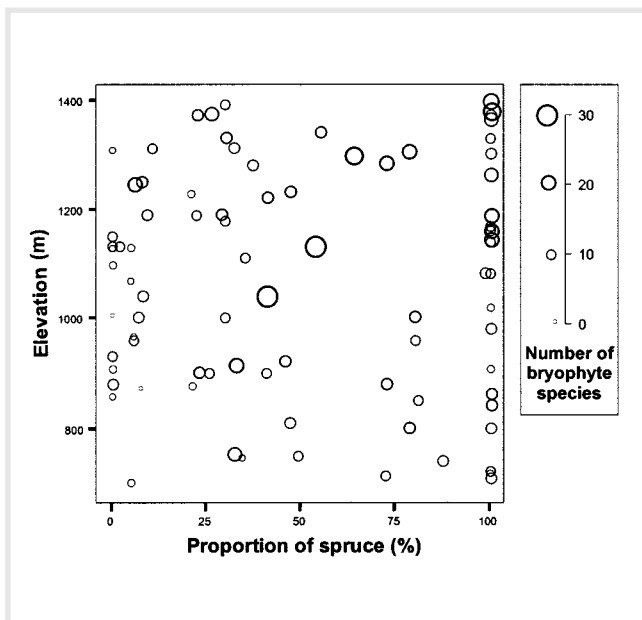
stands. Because common "raw humus species" such as *Vaccinium myrtillus* L. tend to have shallow root systems (Polomski and Kuhn 1998), they are more likely to respond to the observed superficial changes in soil chemistry than deciduous forest species. Thanks to the weak response of vascular species composition, floristically defined community types can be delimited and understorey plants can be used as ecological indicators regardless of past changes in tree species composition. However, the occurrence of *Vaccinio-Piceetea* species and bryophytes in particular can lead to misclassifications in phytosociological site mapping, which should always be complemented by physiographic methods of soil and relief interpretation (Ewald 1999).

As the comparison between the two modes of calculation indicates, the decrease in the reaction indicator value under Norway spruce is mostly due to acidophilous bryophytes. Because Ellenberg's indicator values are based on empirical induction from the ecological behavior of plants in the field (including plant sociology), the effect is conceptually related to the increase in *Vaccinio-Piceetea* species. Insignificantly lower values of *mN* in spruce stands, which correspond to larger C/N ratios in the uppermost soil (Ewald 2000), show that the findings from the Black Forest (Bürger 1991) and Solling (Lücke and Schmidt 1997) are not valid in the part of the Alps under consideration here. The absence of increased eutrophication in spruce stands may be due to relatively low inputs of nitrogen from agriculture and to relatively low levels of disturbance by forest management.
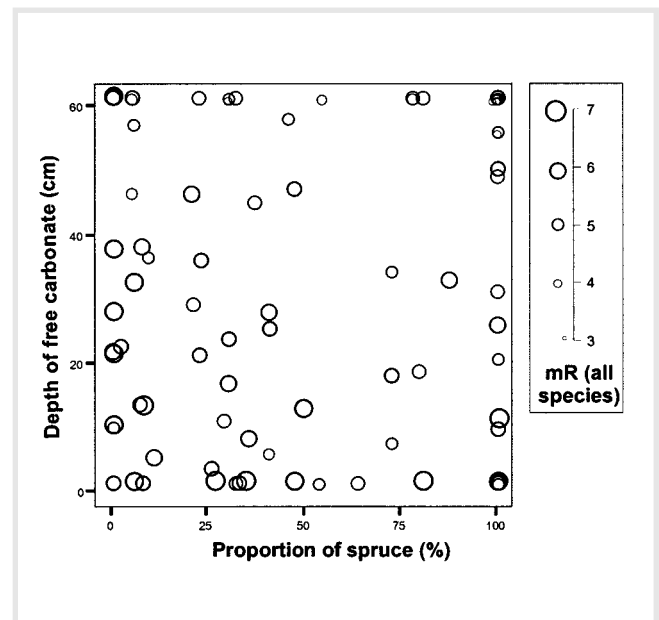

FIGURE 3 Scatterplot showing the proportion of Norway spruce at various elevations, with bryophyte richness depicted as circles.

FIGURE 4 Scatterplot showing the proportion of Norway spruce in relation to the depth of free carbonate in mineral soil, with mean Ellenberg indicator value for soil reaction (calculated on all understorey species) depicted as circles.

Some important conclusions can be drawn for the ecological evaluation of present forest composition in the study area that are likely to be valid in adjacent portions of the northern Calcareous Alps in Austria and Switzerland. As there is no measurable effect of spruce stands on understorey species richness in general and on deciduous forest species in particular, spruce stands do not cause overall impoverishment of the plant communities. Of course, this does not necessarily apply to other guilds and taxonomic groups such as epiphytes, fungi, insects, and mammals. Moreover, there are many good aesthetic, silvicultural, and economic reasons for arguing against single-species tree stands. Sociological and biogeographical species groupings such as "deciduous forest plants" (*Querco-Fagetea*) must be interpreted with care, as there appears to be no stringent functional link to deciduous forest ecosystems.

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