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Environmental and Spatial Influences of Shrub Cover (*Alnus viridis* DC.) on Vegetation Diversity at the Upper Treeline in the Inner Western Alps

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Abstract

Subalpine grasslands in the western Alps are currently facing major environmental changes induced by pastoral disuse. In such a context, the rapid spread of a shrub (*Alnus viridis* [Chaix] DC.) is expected to threaten biodiversity. The aim of this study was to assess the impact of its cover on vascular plant diversity. Data collected at several local levels (108 plots) in a representative area detected a linear decrease in species richness across an increasing *A. viridis* (green alder) cover gradient, whereas alder-stand β -diversity at the community level was particularly singular. We used constrained ordination methods based on Principal Components Analysis to partial out substantial variance explained by spatial structure of samples. The resulting partial Redundancy Analysis accounted for 62.3% of the initial inertia, and the environmental effect by *A. viridis* cover was identified as a major cause of variance in the whole species ordination (16.1%). The expansion of *A. viridis* on subalpine grasslands causes considerable environmental changes which have mostly a negative effect on the conservation of vascular plant diversity in the inner part of the western Alps. However, *A. viridis* appears to contribute to the diversity of the subalpine belt by inducing a peculiar floristic composition.

Introduction

Human impact is recognized as one of the major causes of current environmental changes in most terrestrial ecological systems, and variations in disturbance intensity may strongly alter biodiversity (Huston, 1979; Meyer and Turner, 1994; Vitousek et al., 1997). In mountain areas in particular, a number of authors have suggested that recent pastoral disuse in the subalpine belt has led and/or will lead to a substantial rise in the treeline (Carcaillet and Thinon, 1996; Moir et al., 1999), whereas others have emphasized the effect of global climatic change to explain this phenomenon and to a greater extent the upward shift of mountain plants (Grabherr et al., 1994; Hättenschwiler and Körner, 1995; Pauli et al., 1996; Rolland et al., 1998). In a study comparing both effects, Hofgaard (1997) showed that pastoral intensity was likely to override climatic change in explaining vegetation changes in Norway's subalpine zone, demonstrating that such a variable should be taken into account when studying biodiversity changes in mountain areas. This is particularly obvious in the Alps, where the relationships between shrub density and vegetation diversity at the upper treeline are much dependent on human pastoral activities.

The green alder (*Alnus viridis* [Chaix] DC.) is a widespread shrub in the Northern Hemisphere, including American, Siberian, and European subspecies fully described by several authors (Furrow, 1979; Moiroud and Capellano, 1979; Richard, 1990; Matthews, 1992). It has been classified as a "horizontal competition strategist" *sensu* Mallik et al. (1997) because of the relatively short height of individuals (<4 m) and the dense cover of its foliage. These traits may explain how *A. viridis* can strongly impede the recruitment of tree species such as *Picea* sp. in mesic environments, although such negative interaction can be reversed into facilitation in harsher environmental conditions (Walker and Chapin III, 1986; Callaway and Walker, 1997).

In the Alps, *A. viridis* is naturally restricted to steep, north-facing subalpine slopes on well-drained soils also exhibiting high water availability (Richard, 1990). However, the species has been shown to take advantage of current land disuse and is now spreading on more gentle slopes (Didier and Brun, 1997). Its ability to invade seminatural grasslands may primarily be explained by its strong colonization ability, including high seed production and dispersal (Farmer et al., 1985).

We hypothesized that *A. viridis* expansion on subalpine grasslands is potentially responsible for considerable changes in the biodiversity of the treeline area in the Alps, especially in the rain-shadowed part of this mountain range (inner zone *sensu* Ozenda, 1985) where gradients of edaphic and atmospheric humidity display strong amplitude (Pache et al., 1996; Michalet et al., 2002a). A recent study described the negative impact of dense *A. viridis* cover on arthropod biomass and diversity and hypothesized a reduction in arthropod diversity at the local level subsequent to the expansion of *A. viridis* on abandoned subalpine grasslands (Anthelme et al., 2001). However, knowledge of the impact of expansion of *A. viridis* on the biodiversity of ecological systems remains limited.

In this paper we investigate the changes in vascular plant diversity induced by a gradient of *A. viridis* cover from herbaceous vegetation to dense alder stand. Our method was based on (1) the assessment of changes in species richness induced by *A. viridis* at the plot and community levels using diversity indices, and (2) variance partitioning of the effects of spatial and environmental variables on species ordination, using direct ordination methods. We focus on the following: (1) identifying and quantifying two components of diversity (α and β diversity) affected by alder expansion at several spatial levels; and (2) determining the relative environmental and spatial influences of *A. viridis* cover on vegetation diversity.

We discuss the management implications of the results for plant diversity conservation, with special attention to reversibility processes after alder-stand clear-cutting and to critical cover rate values on which species diversity and abundance are most dependent. Such a model of shrub expansion is intended to be applicable to the inner zone of the western Alps, shown to include large areas with strong potential for expansion of *A. viridis* (Richard, 1967).

Materials and Methods

STUDY AREA

We analyzed the impact of *Alnus viridis* on plant diversity in the area named l'Art (approx. 2 km²), located at the northern limit of Vanoise National Park, Savoie, France (45°35'33"N; 06°52'29"E). L'Art is intended to be representative of *A. viridis* expansion on subalpine grasslands due to its environmental (biotic and abiotic) characteristics. The site is located in a rain-shadowed area as indicated by the high value of the index of precipitation continentality (Gams angle = 55°; see Pache et al., 1996, for a description of this index). The relatively low average annual rainfall (1.3 m yr⁻¹) should limit the expansion of *A. viridis* but is balanced by an important water supply from the Mont-Pourri glaciers (3776 m). Environmental factors associated with the reduction in traditional pastoral intensity have been argued to be responsible for the expansion of *A. viridis* on subalpine grasslands in the area, which has reached at least 10% within the last 50 yr (Wlérick, 1998).

Subalpine grasslands of l'Art are dominated by *Trisetum flavescens* and *Agrostis capillaris*, which are dominant grasses on nitrogen-rich soils, i.e., *Trisetum flavescens* phytosociological association (Favarger and Robert, 1995). Nevertheless, the occurrence of patches of *Nardus stricta* as well as heath species such as *Vaccinium uliginosum*, *V. myrtillus*, and *Rhododendron ferrugineum* also indicates the presence of relatively nutrient-poor soils. *Alnus viridis* is by far the major component of the shrub-arboreal layer, with *Salix appendiculata*, *Sorbus aucuparia*, and *Picea abies* as less dominant species.

SAMPLING DESIGN

In July and August 1998, 108 floristic plots were sampled. In order to avoid errors induced by variation in sample size (Magurran, 1988), each plot was a square of 225 m² area. This size was deemed to be appropriate for plots with dense *A. viridis* cover.

Plots were sampled in three groups (N = 36, 8100 m²) representing three different stages of *A. viridis* expansion on subalpine grassland (Fig. 1):

1. Grassland stage (G), dominated by herbaceous vegetation, with occurrence of isolated young *A. viridis* individuals.
2. Mosaic stage (M), containing equal cover of herbaceous vegetation and *A. viridis*.
3. Alder-stand stage (A), where *A. viridis* cover occupied approximately 80% of the area.

A group of nine additional contiguous plots named "clear-cut stage" was selected close to l'Art in the same environmental conditions as the 108 plots (C in Fig. 1). A dense *A. viridis* stand had been clear-cut in these nine plots 2 yr before floristic assessment.

Plot altitude ranged between 1850 and 2000 m a.s.l., i.e., completely within the subalpine belt in this region. Mean ex-

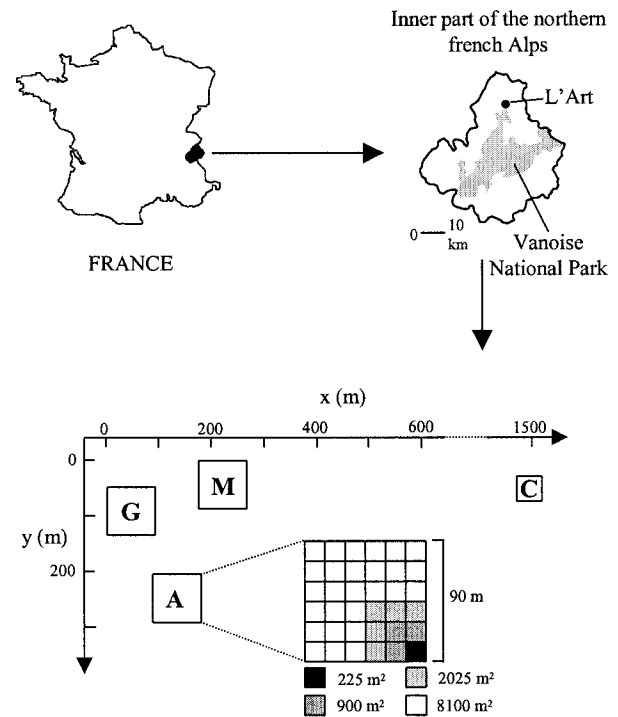


FIGURE 1. Sampling design in l'Art, 117 plots of 225 m², in four vegetation stages. Stages located with (x,y) coordinates (x origin: plot 1 of grassland stage; y origin: plot 1 of mosaic stage). G: grassland stage (36 plots); M: mosaic stage (36); A: alder-stand stage (36); C: clear-cut stage (9). Distances over 240 m (M and C stages) standardized at this value.

posure was 70°, and slope gradient varied from 25 to 40°. Soils were related to Dystric Cambisol (F.A.O., 1998) on gneiss and micaschist bedrock.

ENVIRONMENTAL AND SPATIAL VARIABLES

Vegetation was sampled using a 6-point cover scale for species abundance: +: rare; 1: <5%; 2: 5–25%; 3: 25–50%; 4: 50–75%; 5: >75%; Latin names were used for plants in accordance with the *Flora Europaea* nomenclature (Tutin et al., 1993). In addition, percent cover of *A. viridis* was estimated in the field. Virtual cover values before clear-cutting were assessed for the nine additional plots; they were estimated using residual stem density.

Spatial explanatory variables were *x* and *y* spatial coordinates (m) for each plot. The average distance between centers of plots within each stage was 15 m (see Fig. 1). At distances over 240 m, autocorrelation phenomena between plants have been shown to remain constant (Legendre and Fortin, 1989). Therefore, we deliberately retained this value as a maximum distance between plots, even when minimal distances between stages exceeded 240 m.

DIVERSITY INDICES

As an α -diversity index, species richness was examined along an increasing *A. viridis* cover gradient (%) for the three main groups of plots ($n = 108$). Results were presented at several local levels, i.e., 225 m² ($n = 36$, plot level), 900 m² ($n = 9$), 2025 m² ($n = 4$), and 8100 m² ($n = 1$, stage level), and related to linear and quadratic functions. Comparisons of species richness in response to plot area were performed between grass-

land, mosaic, and alder-stand stages and related to both linear and logarithmic functions. Significance was assessed using the Wilcoxon signed ranks test as samples were related by area class. The significance of coefficients of determination (R^2) was given with the results of F -tests.

The Dice similarity index (Saporta, 1990) was used as a β -diversity index to compare resemblances between floristic composition of stages, including clear-cut stage:

$$D_{ij} = \frac{2a}{2a + b + c}$$

- a = species common to plots in groups i and j;
- b = species exclusively in i plots;
- c = species exclusively in j plots.

ORDINATION METHODS

Multivariate analyses were performed to determine the impact of *A. viridis* on the ordination of all other species, using ADE-4 software (Thioulouse et al., 1997). The contribution of *A. viridis* in the plots-species matrix was removed, as it was considered to be an environmental explanatory variable. Considering that the aim of this study was to determine the impact of *A. viridis* cover on vascular plant diversity, we applied the hypothesis that species responses were linear functions of such a variable. Consequently, Principal Components Analysis (PCA) was selected over Correspondence Analysis (CA), useful when species response to environment is expected to be unimodal (Borcard et al., 1992). PCA on a covariance matrix was performed on the plots-species matrix, including the clear-cut stage (9 plots, total: 117 plots).

VARIANCE PARTITIONING

The sampling design was likely to incorporate substantial spatial autocorrelation generated by the adjacency of plots of the same stage, particularly compared with distances between plots of different stages (see Fig. 1). Because such strictly spatial variance could lead to an overestimation of the strength of the relationship between species and environmental variables (Legendre and Fortin, 1989), it needed to be quantified and, if significant, removed statistically. This can be accomplished with multivariate analysis, using (x, y) coordinates of plots, particularly when the sampling design is regular (see Thioulouse et al. [1995] for a review).

The method selected here consisted of considering (x, y) and their squares and cross-products as a set of spatial variables, as in Wartenberg's Canonical trend surface analysis (Wartenberg, 1985). A cubic function of the coordinates (Borcard et al., 1992) was not included as (1) it was not expected to be significant due to the homogeneous sampling domain, and (2) it introduced

TABLE 1

Distribution of sampling plots by four *A. viridis* cover classes, so as to build the variable "A. viridis cover" used in constrained ordination methods

Cover Classes	Relative Frequency	Minimal Cover (%)	Maximal Cover (%)
1	0.39	0	7
2	0.18	10	50
3	0.19	55	80
4	0.24	85	100

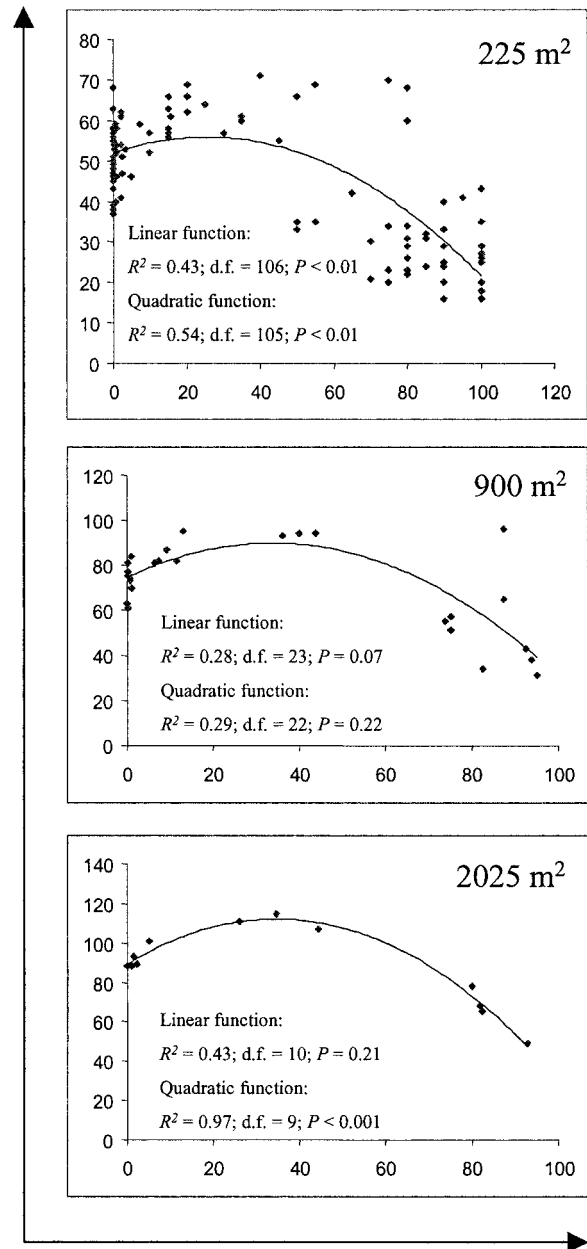


FIGURE 2. Regressions between *A. viridis* cover (%) and species richness using linear and quadratic models. Comparison of three plot levels: 225 m², 900 m², 2025 m².

more arbitrary choices, i.e., more spatial dependent variables, into the analysis (Thioulouse et al., 1995). Quantification of the set of spatial explanatory variables was given by Redundancy Analysis (van den Wollenberg, 1977), which is the constrained form of PCA.

The effects of *A. viridis* cover on plot ordination after spatial variance had been removed were determined using partial RDA (Borcard et al., 1992), with spatial explanatory variables as covariables, and *A. viridis* cover as a single constraining variable in four classes (Table 1). In turn, partial RDA with *A. viridis* cover as a covariable was conducted to identify and remove spatial variance not shared with *A. viridis* cover.

The significance of the deviation in variance explained by each variable was tested using a Monte Carlo randomization test, which compared variance from that explained by a random var-

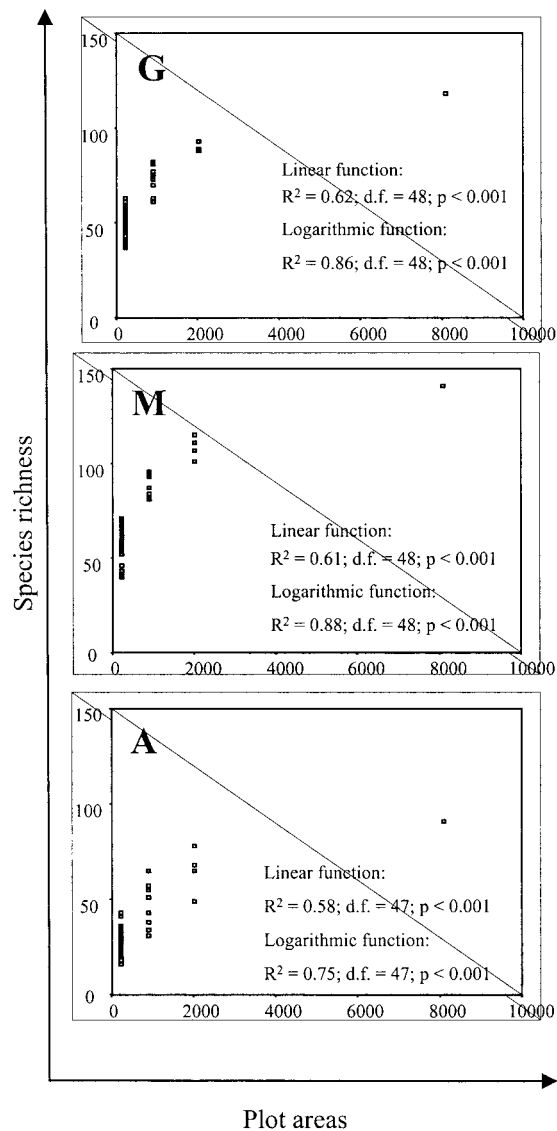


FIGURE 3. Comparative species richness of three vegetation types related to plot area (225 m²: n = 36; 900 m²: n = 9; 2025 m²: n = 4; 8100 m²: n = 1) following linear and logarithmic models. G: grassland; M: mosaic; A: alder stand. Only 47 d.f. in A because one 225-m² plot has been removed (situated on a cliff, not representative of the alder stand).

iable with 1000 permutations (Romesburg, 1985; Økland and Eilertsen, 1994).

Results

SPECIES DIVERSITY INDICES

A total of 185 species was recorded in 108 plots. At the plot level (225 m²), species richness decreased significantly with increasing *A. viridis* cover (Fig. 2). This relationship was considered to be linear ($R^2 = 0.43$, $P < 0.01$) as the variance explained was roughly comparable to a quadratic model ($R^2 = 0.54$, $P < 0.01$). With respect to the other levels, species response to *A. viridis* cover was unimodal at 2025 m² ($R^2 = 0.97$, $P < 0.001$) and reached a peak at 25 to 30% cover, whereas neither linear nor quadratic models were significant at 900 m².

Within each stage, the response of species richness to sample area followed a logarithmic curve model (Fig. 3). However, linear models could not be rejected because significant R^2 values

TABLE 2

Significance of species richness variation between plots in stages for four area classes (cf. Figure 3) analyzed with Wilcoxon signed ranks test^a

Couples of Stages	Negative Ranks	Positive Ranks	Z ^b	P
G-M	44	6	-5.27	<0.001
M-A	0	50	-6.16	<0.001
G-A	1	49	-6.16	<0.001

^a Abbreviations: G = grassland stage, M = mosaic stage, A = alder-stand stage.

^b Based on negative ranks.

ranged from 0.58 in the alder-stand stage to 0.62 in the grassland stage. The alder-stand stage appeared to yield the lowest richness values regardless of area, whereas the mosaic stage was the richest stage. Wilcoxon tests showed that differences in species richness between stages were significantly different regardless of plot size (Z-values in Table 2). Specifically, all the mosaic plots were richer than the alder-stand plots.

Grassland and mosaic stages were by far the most similar with β -diversity between their stages of 0.78 (Table 3), whereas grassland and alder-stand stages yielded the greatest difference (0.44). The clear-cut stage displayed approximately identical similarity indices regardless of the stages with which it was compared.

PLOT ORDINATION ON PCA AND PARTIAL RDA

Multivariate analyses were performed on 117 plots and 194 plant species. Both PCA and partial RDA with spatial variables as covariables displayed two emergent axes (see eigenvalues on Fig. 4). PCA yielded a complete separation of stages (Fig. 4a). On the first axis, the grassland and mosaic stages had negative scores, whereas both the alder-stand stage and the clear-cut stage had very similar positive scores. Axis 2 separated the grassland and mosaic stages.

However, partial RDA displayed a less distinct separation of stages (Fig. 4b) due to substantial variance explained by the covariable. The alder-stand, grassland, and clear-cut stages were close to each other and were mostly or entirely overlapped by the mosaic stage. *Alnus viridis* was positively correlated ($R^2 = 0.47$, $P < 0.001$) with plot scores on the first axis; conversely, there was no significant relationship between axis 2 and *A. viridis* cover ($R^2 = 0.00$, $P = 0.5$).

VARIANCE PARTITIONING

The fractions of variance in species abundance explained by *A. viridis* cover and/or the set of spatial explanatory variables were as follows:

TABLE 3

β -diversity values between stages using Dice similarity index D_{ij}^a

Stages	G	M	A	C
G	1			
M	0.78	1		
A	0.44	0.52	1	
C	0.51	0.58	0.55	1

^a Abbreviations: G = grassland stage, M = mosaic stage, A = alder-stand stage, C = clear-cut stage.

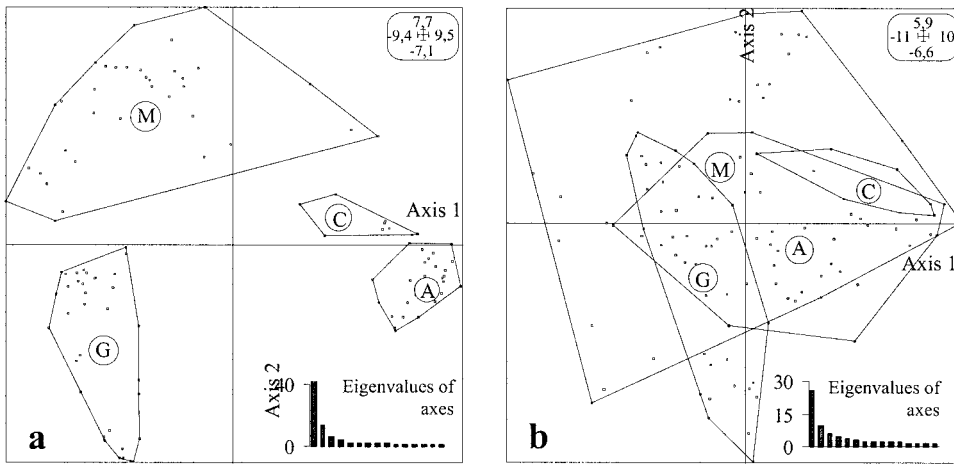


FIGURE 4. Plot ordination diagrams extracted from PCA: (a) before partialling out a set of spatial coordinates (x , y , x^2 , y^2 , xy) with partial RDA (Inertia: 113.98), (b) after partialling out (Inertia: 73.96). Plots belonging to stages are passively added with convex hulls: G: grassland stage, M: mosaic stage, A: alder-stand stage, C: clear-cut stage.

- Variance explained by *A. viridis* cover (A) = 35.1% (1).
- Variance explained by set of spatial explanatory variables (B) = 37.7% (2).
- Variance explained by A not shared by B = 16.1% (3).
- Variance explained by B not shared by A = 18.8% (4).

According to these results, the distribution of the total variance of the analysis was displayed in Fig. 5. Strictly environmental effects of *A. viridis* cover on species abundance reached 16.1% of total variance (3), whereas *A. viridis* cover related to spatial variables accounted for 19%, given by (1)–(3). Effects of coordinates not related to *A. viridis* cover were responsible for 18.8% of total variance (4).

CRITICAL VALUE OF *A. VIRIDIS* COVER

The variance of species abundance explained by *A. viridis* cover variable divided into two classes was displayed in Table 4 for eight critical values; only grassland, mosaic, and alder-stand stages were considered (108 plots). The relationship was unimodal ($R^2 = 0.88$, $P < 0.01$), and the greatest amount of explained variance was found at a critical value of 45% cover. From 25 to 65% cover, *A. viridis* explained more than 30% of the species ordination.

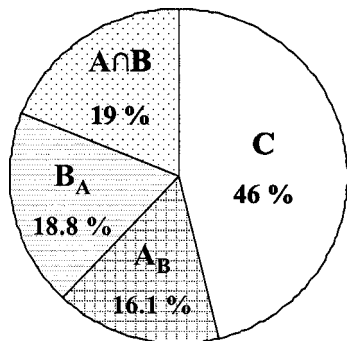


FIGURE 5. Percentage of variance of the species data matrix (PCA plots-species) explained by geographical coordinates and *A. viridis* cover. A_B : variance explained by *A. viridis* cover not shared with set of coordinates; B_A : variance explained by the set of coordinates, not shared with *A. viridis* cover; $A \cap B$: variance shared by the two variables; C: undetermined.

Discussion

QUANTIFYING THE INFLUENCE OF *A. VIRIDIS* COVER ON VEGETATION

Although species richness does not completely account for the response of species diversity to environmental changes (Ganeshaiah and Shaanker, 2000), it remains a powerful indicator widely used (Tilman and Pacala, 1993; Knops et al., 1999; Ohl-muller and Wilson, 2000). Our results showed that the response of species richness to increasing *A. viridis* cover at the plot level was strong and separated into two trends (Fig. 2): (1) a rise at low cover values, and (2) a severe decrease starting at 25 to 30% cover. This dual effect, similar to the hump-backed model described by Al-Mufti et al. (1977), is considered a classical model of secondary succession (Tatoni et al., 1994; Gillet et al., 1999; Michalet et al., 2002b). It commonly provides a basis for assuming a unimodal relationship between species richness and colonizing species likely to be analyzed by CA. However, our results showed that the second effect was much stronger than the first effect, which was relatively negligible at the plot level. That is why the resulting relationship could be described by a linear function and justified the use of PCA in further analyses (e.g., Dolédec et al., 2000).

The unimodal trend was most marked at 2025 m² (Fig. 2), suggesting that the response of species richness to fragmentation was positive at higher spatial levels. This hypothesis was strengthened by the significantly higher richness values observed in the mosaic stage, independently of the selected area (Fig. 3). However, the alder-stand stage remained species-poor at higher spatial levels, which was interpreted as a confirmation of the negative influence of dense and large alder stands on species richness.

The improved degree of explanation given by logarithmic R^2 compared to linear R^2 in every stage was not sufficient to detect any *A. viridis* cover effect on saturation of species richness, which is considered a relatively rare phenomenon in vegetation communities (Cornell, 1999). However, saturation was hypothesized to potentially occur on a regional scale in dense alder stands, on the grounds that the largest spatial level assessed at each stage was underestimated (8100 m², $n = 1$) and had a relatively low value in the alder-stand stage (Fig. 3).

The negative effects of *A. viridis* on species richness were likely generated by a loss in the spatial diversity of habitats (Tilman and Pacala, 1993). This type of homogenization process is commonly observed in dense deciduous forests (Grimmond et

TABLE 4

Comparison of the variances explained by *A. viridis* cover divided into two varying classes in PCA. Relation between variances and critical values: Quadratic $R^2 = 0.88$, $P < 0.01$. Significance of each variance tested by randomization test on 1000 permutations.

Critical <i>A. viridis</i> Value (%)	Variance Explained	<i>n</i> (below critical cover)	<i>n</i> (over critical cover)	X > obs (1000 permutations)
5	0.249	45	63	0
15	0.257	51	57	0
25	0.314	58	50	0
35	0.33	62	46	0
45	0.338	64	44	0
55	0.327	70	38	0
65	0.31	71	37	0
75	0.231	78	30	0

al., 2000). It is hypothesized to be especially important for *A. viridis*, which develops a high density of foliage and stems, demonstrated experimentally to be denser than those of other colonizing shrubs (Mallik et al., 1997). The resulting cover accounts for reductions in light availability, and in temperature and atmospheric humidity ranges that have been observed by Richard (1968). However, considering similarities at the community level (β -diversity), the strong differences between the alder-stand and the other stages indicated the establishment of a new vegetation community and therefore suggest the occurrence of a positive effect of the alder expansion on vegetation diversity.

SEPARATING SPATIAL AND ENVIRONMENTAL EFFECTS OF *A. VIRIDIS* COVER

Multivariate analyses are generally known to be “attractive methods in that they provide an overall significant test of vegetation change” (ter Braak and Wiertz, 1994). Moreover, the methods used in our study allowed us to partial out variables from the entire analysis. As suggested by Borcard et al. (1992), variables considered as environmental may be partly due to the spatial structure of the sampling scheme. With respect to the results in Figure 5, this was particularly obvious for *A. viridis* cover, which explained 16.1% of the total variance by means of its environmental effects whereas 18.8% was linked to spatial structure.

To assess the environmental effects of *A. viridis* on species data, quadratic effects of (*x*, *y*) coordinates were removed with partial RDA. The appropriateness of such an analysis was indicated in Figure 4b by the fact that the grassland and the alder-stand stages were partly inserted into the mosaic stage, which included both plots dominated by herbaceous vegetation and *A. viridis*. Conversely, such insertion was not observed before partialing out spatial effects (Fig. 4a).

Compared with general cases of grassland colonization by native species, our results stressed the singular importance of *A. viridis* cover in modifying plant vascular diversity. Its strictly environmental effect is the principal factor of species ordination before slope gradient and other abiotic factors (unpublished data), and it is attributed to a considerable homogenization process (see Mallik et al., 1997) in a particularly heterogeneous area, the subalpine belt. Other native species in the Alps such as *Brachypodium pinnatum* and *Rhododendron ferrugineum* have also been demonstrated to display strong negative impacts on plant diversity at high cover densities (Bobbink and Willems,

1987; Escaravage et al., 1996). Therefore, the terms “monotypic” (Parker et al., 2000) or alternatively “monopolistic” may be used to define such a group of native species which colonize herbaceous areas following major environmental changes, and generate such dense cover that they prevent most species from spatially coexisting.

IMPLICATIONS FOR THE SUSTAINABLE CONSERVATION OF PLANT DIVERSITY

Large areas of alder stands are currently managed in the western Alps, particularly to favor *Tetrao tetrix* habitats that need to be fragmented for the bird’s survival (Combes, 1997; Anthelme et al., 2001). Our results concerning the clear-cut stage showed that 2 yr after clear-cut, species abundances remained similar to those of dense alder-stand stage (Fig. 4b). This showed that the recovery of subalpine grasslands from dense alder stands could be a very slow process. Because cover is no longer an effective explanation, the hypothesis that this similarity persists due to nitrogen soil enrichment produced by symbiosis between *A. viridis* and the actinomycete *Frankia* sp. (Moiroud and Cappellano, 1979; Huss-Danell, 1997) should be investigated for future research.

In our opinion, efficient management, if proven necessary, should be aimed towards fragmented alder stands, whose floristic composition is probably more easily reversible. Results identified the *A. viridis* cover of 45% as the critical value at which species abundances were the most distinctively different (Table 4). Accordingly, potential management could be applied at such a cover, although the results require greater corroboration. As shown for the effects of *Larix decidua* cover on vegetation diversity (Gillet et al., 1999), *A. viridis* cover of 25% generated the highest species richness found at the plot level (Fig. 2). This value should consequently be viewed as a management target when the conservation of plant diversity is the concern in a context of subalpine grassland colonization by *A. viridis* in the inner part of the western Alps.

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