

Unexpected impacts of climate change on alpine vegetation

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The vegetation in a high alpine site of the European Alps experienced changes in area between 1953 and 2003 as a result of climate change. Shrubs showed rapid expansion rates of 5.6% per decade at altitudes between 2400 m and 2500 m. Above 2500 m, vegetation coverage exhibited unexpected patterns of regression associated with increased precipitation and permafrost degradation. As these changes follow a sharp increase in both summer and annual temperatures after 1980, we suggest that vegetation of the alpine (2400–2800 m) and nival (above 2800 m) belts respond in a fast and flexible way, contradicting previous hypotheses that alpine and nival species appear to have a natural inertia and are able to tolerate an increase of 1–2°C in mean air temperature.

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The Intergovernmental Panel on Climate Change (IPCC) determined that, during the 20th century, global air temperature warmed by an average of $0.6 \pm 0.2^\circ\text{C}$ (95% CI; IPCC 2001). This pattern was not uniform over the planet and, in the European Alps, the increase in air temperature was more than twice as great as the increase in global mean air temperature (Böhm *et al.* 2001). Neither were changes in the precipitation regime spatially or temporally uniform; in the central Alps, precipitation increased by up to 10% between 1900 and 2000 (IPCC 2001).

There is ample evidence to indicate that recent climatic changes have affected a broad range of organisms, with consequences that are already discernible in phenology and distribution of species, community composition, and ecosystem structure and dynamics (Walther *et al.* 2002). Quantitative estimates of such biological impacts have led to the recognition of a climate change “fingerprint”, with greater amplitude expected at high latitudes and altitudes (Root *et al.* 2003).

In alpine environments, abiotic factors, especially climate, dominate biotic interactions. Although the impact of short-term climatic fluctuations on alpine vegetation is expected to be negligible because of the slow growth rates and extended life cycles of species (Pauli *et al.* 1999), high altitude vegetation is anticipated to be more sensitive to long-term climate change (Gottfried *et al.* 1998; Theurillat and Guisan 2001). Evidence of the sensitivity of alpine habitats is provided by shifts in the altitudinal-range margins of plant species and bioclimatic zones in the past 50 years, with upward displacement of 120–340 m for tree and woody shrub species (Kullman 2002), upward migration of alpine and nival plant species at a rate of 8–10 m per decade (Grabherr *et al.* 1994;

Walther *et al.* 2005), and changes in community composition (Keller *et al.* 2000).

In the Alps, landscape changes are complicated by the millenia-old influence of human activities, making it difficult to distinguish between the effects of climate warming and land-use modification. However, the alpine (2400–2800 m above sea level [asl]) and nival (> 2800 m asl) belts – where anthropogenic land-use effects are negligible – provide natural models of change that are exclusively influenced by climate warming (Keller *et al.* 2005). Indeed, the alpine–nival ecotone may serve as an early indicator of climate-change impacts, because even small-scale migration is likely to cause fundamental changes in species composition (Gottfried *et al.* 1998).

The effects of climate change are likely to be detectable at lower tiers of ecological organization (eg species composition, functional pathways) before affecting higher-level ecological systems (Neilson 1993). In this paper, we focus on high altitude habitats and investigate the level of ecological hierarchy at which climate change can be seen, by analyzing changes in vegetation distribution, community dynamics, and vegetation series (ie shrublands, grasslands, wetlands) in the Italian Alps for the period 1950–2003.

The study area was located around Stelvio Pass (46°31' N, 10°25' E; elevation 2230–3094 m asl; investigated area 5.6 km²), a high alpine site in Stelvio National Park in the Italian Central Alps. At the elevation of our site, the only anthropogenic land use is extensive summer pasturing. Historical archives indicate that pasturing has remained nearly constant since 1950, allowing us to exclude land-use change as a driver of vegetation change since that time.

■ Methods

Using GIS, we compared a phytosociological map from 1953 (Giacomini and Pignatti 1955) with a new map that we constructed in 2003. The 1953 map and the 2003 map

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drawn in the field were both scanned at high resolution and geocoded using the same software, ArcView GIS 3.2. Vegetation changes were calculated using three different measures: coverage, dynamics, and ecological series. Changes in coverage were classified into three groups: bare ground, discontinuous vegetation, and continuous vegetation. Vegetation dynamics were linked to successional changes and/or invasion by associations of plants from different altitudinal belts. The ecological series of habitat types were calculated using the seven main vegetation series (shrublands, grasslands, wetlands, snowbeds, pioneer, other, bare ground). The vegetation changes (in coverage, dynamics, and ecological series) were measured with reference to area (ie increase in area, no change in area, decrease in area) and to elevation (ie upward extension, no altitudinal change, downward extension).

Air temperature and precipitation records for the study period were provided by the two closest available stations, Sils (located 50 km from the study area, at 46°26' N, 9°46' E; elevation 1798 m asl; Begert *et al.* 2005) and Silandro (located 25 km from the study area, at 46°37' N, 10°46' E; elevation 718 m asl). For snow cover, data from 1978 onward were provided from the closest available station, Cancano (located 9 km from the study area, at 46°31' N, 10°18' E; elevation 1948 m asl).

Results

The climatic conditions of the Alps changed between 1950 and 2003 (Figure 1). The mean annual air temperature increased, with a more pronounced rise since 1980, at Silandro (+1.0°C) and Sils (+1.2°C). The seasonal patterns of air temperature indicate an overall increase for summers (June–August) at both stations, with a sharp increase after 1980 (+1.1°C 1990–1999 at Silandro, +0.42°C 1980–89, and +1.02°C 1990–99 at Sils, relative to 1961–1990 averages), conforming to a trend described for the whole of Switzerland (Begert *et al.* 2005).

The precipitation pattern is less clear, with large fluctuations within the considered time span. Total precipitation increased, especially after 1980 (+10% at Silandro and +7% at Sils with respect to the reference values of 1961–1990), in agreement with Walther *et al.* (2002), who identified a 10% increase in precipitation. The seasonal patterns also indicated a general increase in precipi-

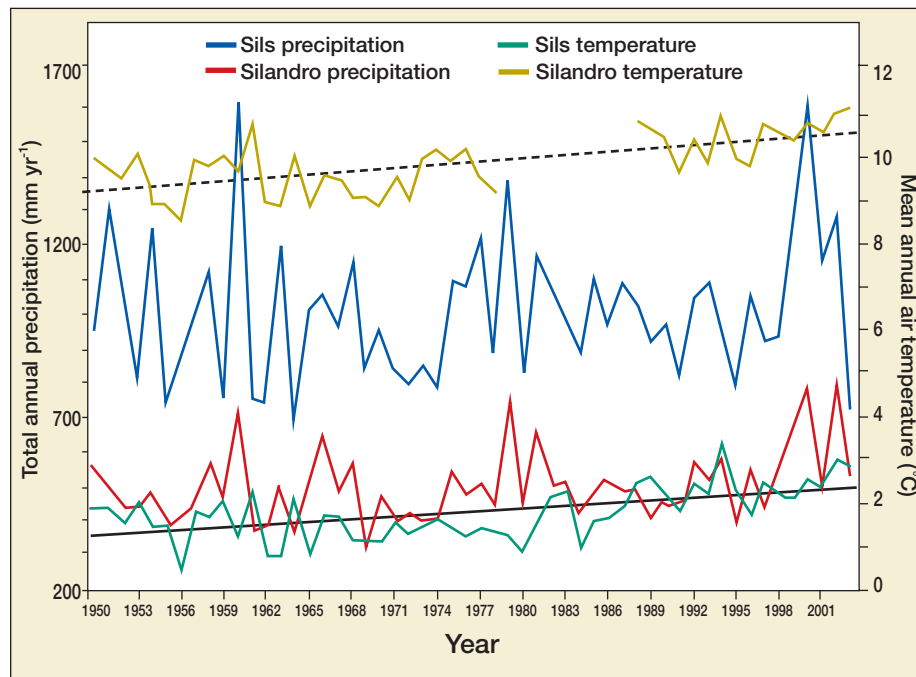


Figure 1. Climate data from 1950 to 2003: mean annual air temperature (°C) at Silandro (elev 718 m asl; yellow) and Sils (elev 1798 m asl; green) and total annual precipitation (mm yr⁻¹) from 1950 to 2003 at Silandro (red) and Sils (blue). The linear regressions (black dashed line for Silandro and solid black line for Sils) highlight the substantial increases in temperature recorded at the two sites.

itation, except in the winter season, which showed a remarkable decrease, with the lowest values occurring in the past decade. Since 1978, the snow depth recorded at Cancano decreased and the length of the snow season shortened as well (Figure 2), due to summer warming and a reduction in snow fall.

Climate warming induced permafrost degradation, as indicated by the thermal profile within a deep borehole located 1 km east of Mt Scorluzzo. We observed an increase in permafrost temperature of 1.2°C since 1950 (Guglielmin 2004). The last glacier body (located in the study area on the northern slope of Mt Scorluzzo) completely disappeared between 1930 and 1958.

The vegetation changes between 1950 and 2003 show a general pattern of increase in coverage, with a shift toward late successional and climax stages, the appearance of communities from the lower altitudinal belts, and upward displacement of shrublands to 2500 m asl. Above this threshold, there are contrasting patterns, with the same expected impacts as recorded below, but with some unexpected regressions and decreases in coverage. The changes in coverage type indicated that, over the whole area, increases exceeded decreases (22.1% versus 11.6%); overall, spatial patterns were heterogeneous (Figure 3a). The greatest change occurred between 2230 and 2500 m and was associated with an increase in coverage, mainly from discontinuous to continuous vegetation, although there are patchy areas where coverage decreased. Above 2500 m, the increase in coverage was more modest, with

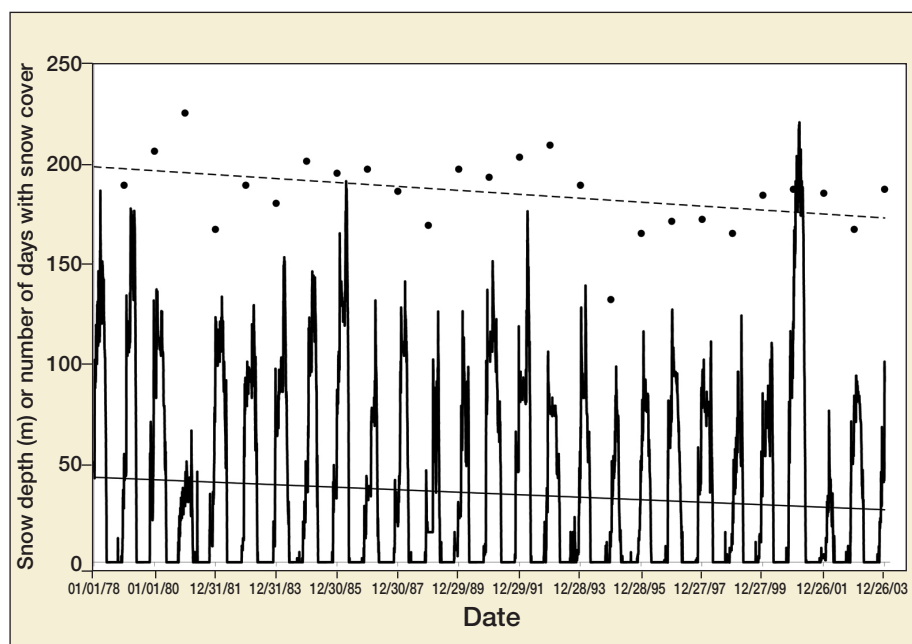


Figure 2. Snow patterns recorded at Cancano between 1978 and 2003, with the daily snow depth measured at the ground (solid thick line) and its linear regression (solid light line), the total number of days with snow cover per year (black dots) and its linear regression (dashed line). Despite the high annual variability of the snow depth, the general pattern shown by the linear regression indicates a decrease in both snow depth and snow permanence.

the exception of 2650–2700 m and above 2800 m, where there was a decrease in coverage.

The vegetation dynamics of the area as a whole indicate similar patterns of change, with expansion exceeding regression (34.8% versus 20.2%). The spatial distribution of the changes (Figure 3b) indicates that expansion largely prevails between 2230 and 2500 m asl, whereas, above 2500 m, expansion was slightly greater than or equal to regression. These patterns suggest that the changes in distribution are often asymmetrical, with species invasions from lower elevations moving faster than the upslope retreat of resident species (Walther *et al.* 2002).

The changes in the ecological series indicate a cascade effect (Table 1), with the arrival of the alpine shrubland and upward displacement of the alpine grassland (especially between 2230 and 2500 m). The shrub invasion is due to the expansion and upward displacement of the

pre-existing association, dominated by the dwarf shrub *Loiseleuria procumbens*, and by the arrival of vegetation from the sub-alpine belt, an association characterized by *Rhododendron ferrugineum* (Figure 4 a,b). The expansion and upward migration of the alpine shrubland matches similar observations of shrub invasion of grasslands by *Vaccinium uliginosum* in the alpine belt of the European Alps (Bahn and Körner 2003).

The average increase in coverage by shrubs and dwarf shrubs was +1.9% per decade over the whole area, with the highest rates of expansion occurring below 2500 m (+6.6% per decade at 2230–2400 m; +5.6% per decade at 2400–2500 m). This rapid migration of the shrub-line was even greater than that observed in the Arctic, where the cover of tall shrubs in the tundra has increased by 1.2% per decade, mainly in response to summer warming (ranging between 0.15–0.17°C to 0.3–0.4°C per decade; Chapin *et al.* 2005). The sharp increase in summer temperatures (up to +1.1°C per decade) that occurred at our site after 1980 may explain this rapid increase in shrub coverage, despite the summer cooling recorded from 1960 to 1979.

Discussion

The expansion of shrubs within the alpine belt may indicate a modification of the competitive relations among shrub-plant functional types (ie *R ferrugineum*), with dwarf shrubs (ie *L procumbens*) and chamaephytes (ie *V uliginosum*) displacing hemicryptophytes (ie *Carex curvula*), as hypothesized by Theurillat and Guisan (2001). The decrease in the length of the snow cover season may be responsible for the increase in *L procumbens* and *V uliginosum*, which are typical of windswept areas,

Table 1. Changes (%) in the ecological series of habitat types between 1953 and 2003 for various altitudinal ranges

Habitat	2230–2400 m asl	2400–2500 m asl	2500–2600 m asl	2600–2700 m asl	2700–2800 m asl	2800–2900 m asl	Average whole area
Shrubs	+33.3	+28.1	–3.5	–1.3	n/a	n/a	+9.4
Grasslands	–31.3	–30.7	+14.6	–2.3	+9.0	–8.0	–8.1
Wetlands	–6.6	–0.5	–2.2	–2.3	n/a	n/a	–1.9
Snowbed	n/a	–1.6	–14.1	+3.9	+2.4	n/a	–1.6
Pioneer	+2.3	+2.9	+7.1	–5.0	+7.7	–31.0	–2.7
Other	+0.1	n/a	+0.6	n/a	n/a	n/a	+0.1
Bare ground	+2.2	+1.8	–2.5	+7.0	–19.1	+39	+4.7

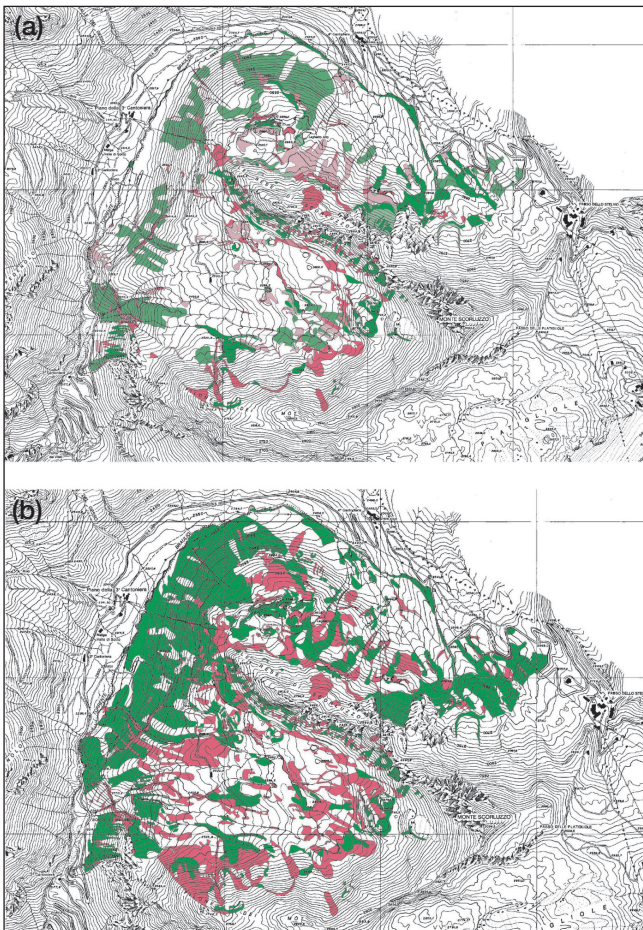


Figure 3. (a) Changes in coverage type between 1953 and 2003 in the Stelvio Pass area (central Italian Alps). Solid magenta = coverage decrease from continuous vegetation to bare ground; magenta stripes = coverage decrease from continuous to discontinuous vegetation; pale magenta = coverage decrease from discontinuous vegetation to bare ground; solid green = coverage increase from bare ground to continuous vegetation; green dots = coverage increase from bare ground to discontinuous vegetation; green stripes = coverage increase from discontinuous to continuous vegetation. (b) Changes in vegetation dynamics between 1953 and 2003 in the Stelvio Pass area (central Italian Alps). Magenta = shift toward early successional and/or pioneer stages of succession (ie from the climax alpine grassland *Caricetum curvulae* to the pioneer vegetation *Oxyrietum digynae*) and/or ingressions of associations from higher altitudinal belts (ie from the alpine grassland to the alpine shrubland); green = shift toward late successional and/or climax stages (ie from pioneer vegetation to climax alpine grassland) and/or ingressions of associations from lower altitudinal belts (ie from alpine shrubland to alpine grassland).

instead of *R ferrugineum*, which requires a longer and thicker snow cover.

There was also an upward migration of the alpine grassland (mainly 2500–2600 m), replacing the snowbeds, which in turn shifted upward (2600–2800 m; Figure 3b; Table 1). Above 2500 m, the alpine grassland was invaded by the alpine shrub *V uliginosum*, which migrated

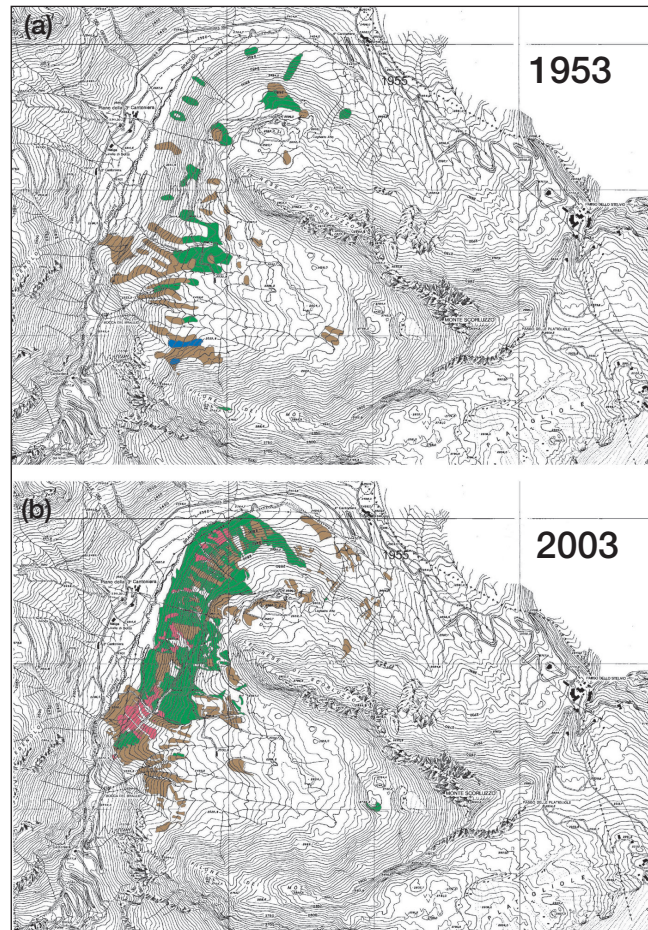


Figure 4. (a) Shrub distribution in 1953 in the Stelvio Pass area (central Italian Alps). Brown = dwarf shrub association (*Loiseleurietum–Cetrarietum*); green = mosaic between the dwarf shrub association (*Loiseleurietum–Cetrarietum*) and the alpine grassland; blue = mosaic between the dwarf shrub association (*Loiseleurietum–Cetrarietum*) and the snowbeds; (b) Shrub distribution in 2003 in the Stelvio Pass area (central Italian Alps). Brown = dwarf shrub association (*Loiseleurietum–Cetrarietum*); green = mosaic between the dwarf shrub association (*Loiseleurietum–Cetrarietum*) and the alpine grassland; magenta = alpine shrub association (*Rhodoreto–Vaccinieta*).

upward to elevations of more than 2650 m.

Overall, the upward movement of the grassland vegetation confirms the ability of late successional species such as *C curvula* to migrate, and corroborates experimental studies suggesting that a moderate warming of 1–2°C may favor upward colonization by alpine climax grassland, dominated by *C curvula*. The contraction of the snowbeds and their shift to higher altitudes is consistent with the shortening of the snow cover season and suggests that species that require long periods of snow cover might find refugia at higher altitudes (Keller *et al.* 2005).

Wetland vegetation also experienced a regression, especially at lower altitudes (Table 1). Pioneer vegetation, on the other hand, showed increased coverage below 2600 m, although there were contrasting and unexpected patterns

above 2600 m; it decreased between 2600 and 2700 m and above 2800 m, but increased between 2700 and 2800 m. In addition, the pioneer vegetation showed a dynamic regression due to invasion by *Androsacetum alpinae*, the earliest colonizer during succession, mainly above 2500 m. Bare ground coverage showed opposite trends with respect to the pioneer vegetation above 2500 m. These results are unexpected in light of simple models which predicted upward displacement of vegetation in response to climate change and of earlier evidence, at the species level, which confirmed an upward migration of alpine and nival species (Grabherr *et al.* 1994; Walther *et al.* 2005), shifting at a rate of 8–10 m per decade on the mountain summits of the Austrian Alps (Grabherr *et al.* 1994).

Hydrological context is particularly important for interpreting the altered spatial distribution of pioneer vegetation. At the lower altitudes, increases in such species were mainly associated with streams and alluvial and debris flow fans, while at the higher altitudes, regressions were mainly seen on steep slopes. Increased summer precipitation and early snow melt may result in greater hydrological disturbance (eg flooding, debris flow), leading to both rejuvenation of vegetation and increased amounts of bare ground. At the higher altitudes, degradation of the permafrost, which has been occurring since 1950 – as documented by the permafrost temperature recorded in a deep borehole at the boundary of the study area (Guglielmin 2004) – may also trigger disturbances, in the form of debris flow and landslides (Williams 1995).

Our results indicate that both the increase in mean annual air temperature of 1.0–1.2°C between 1950 and 2003, the summer warming of 0.4–1°C per decade after 1980, and the shortening of the snow season may activate feedback mechanisms (Chapin *et al.* 2005), able to cause vegetation changes at the community level. According to Neilson (1993), only high levels of climatic change lead to detectable signals in the upper levels of ecological hierarchies. Moreover, Pauli *et al.* (1999) suggest that only long-term climatic changes are able to produce significant changes in vegetation patterns in the alpine and nival belts.

In contrast with most studies on alpine and nival species (Theurillat and Guisan 2001), our data suggest that even 1–2°C warming of air temperature may produce important changes in vegetation community dynamics. In addition to expected effects (eg species and community displacement), unexpected effects may also have unpredictable consequences for biodiversity. For example, increased surface instability and disturbance – which probably caused the unexpected regressions above 2600 m in this study – may create a migration barrier that restricts the colonization of higher altitudes to disturbance-adapted species. As the increase in summer and annual temperatures is almost entirely confined to the past two decades, we suggest that alpine and nival vegetation may respond faster and more flexibly to climatic change than was previously believed to be possible (Pauli *et al.* 1999; Walther *et al.* 2005).

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