Coincidence of the alpine–nival ecotone with the summer snowline

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Abstract

The alpine–nival ecotone is the transition between the lower located alpine grassland/tundra zone and the upper located sparsely vegetated nival zone in the mountains. Its characteristics are qualitatively known. Here we study the dynamics of the ecotone through a quantitative approach based on plant data (from Mt Schrankogel, 3497 m, observations 1994 and 2004) and snow data (from 268 routine climate stations in the Alps, observations 1975–2004).

We introduce the nivality index as the area ratio of nival and alpine plants, and the snow duration as the length of the summer snow cover. We fit a nonlinear probabilistic model to our field data; it yields state functions of both quantities. The nivality index curve comprises the entire information of the plant data in one analytical function; the snow duration curve represents the equivalent for the full snow data set. Thus all relevant parameters of both quantities follow from the respective state function.

We find that the analytical profile of the alpine–nival ecotone at Mt Schrankogel (based on nivality index observations from the altitude interval 2910–3090 m) happens to sit right in the center of the independently determined summer snow profile across the entire Alps; specifically, the central altitude of the Schrankogel ecotone coincides almost perfectly with the central altitude of Alpine5 snow duration. Both state functions show extreme temperature sensitivity at 2967 m (vegetation) and 2897 m (snow), and both altitudes exhibit a positive trend during the measurement period.

Keywords: alpine–nival ecotone, altitudinal species ranges, climate change, temperature sensitivity, high mountain vegetation, nivality index, snow duration, state function, probabilistic model

Online supplementary data available from stacks.iop.org/ERL/6/014013/mmedia

1. Introduction

Mountain plant life is strongly determined by snow [1–7]. Both snow duration and temperature govern habitat suitability [3, 4, 8, 9] and generate the zonal arrangement of altitude-dependent vegetation, a common feature in all mountain systems of the world [10, 11]. Here we focus on the alpine–nival ecotone [3, 4, 12–14]. This is the relatively narrow transition that connects the alpine grassland/tundra zone with the upper sparsely vegetated nival zone. The qualitative concepts for identifying and understanding this phenomenon can broadly be classified as follows:
The ecotone is defined through the position of the permanent snowline. This is a climatological concept based on connecting the remaining traces of the snow pack which survive the average summer [3, 15, 16].

The ecotone is defined through the patchiness of vegetation cover which is not vertically constant but increases from lower to higher altitudes. Following this understanding, the alpine–nival ecotone is located in the zone in which the closed (predominantly alpine) vegetation is gradually replaced by an open (predominantly nival) vegetation [4, 17, 18].

The ecotone is defined through the turnover from alpine to nival plant species. Alpine plants dominate extended regions of dwarf shrub heath or grasslands (alpine tundra) located at lower altitudes while the cryo-tolerant nival plants grow at higher altitudes, in scattered cushion fields, restricted to a few favorable habitats [2, 13, 19, 20].

It is the latter definition that we want to adopt in the present study as qualitative background of the phenomenon. We intend to proceed further by following a quantitative approach. A stringent formalization of the alpine–nival ecotone concept is still lacking in the literature; however, it is urgently needed in the context of current climate impact research concerning mountain systems.

It is our purpose to carry out this task, in a preliminary fashion, by quantifying and theoretically formalizing the state of the alpine–nival ecotone. We shall do this through independently constructing state functions for the mountain vegetation and the snow cover, both depending upon temperature. We shall use mountain vegetation data at one individual Alpine peak (Mt Schrankogel in Tyrol) and snow data for the entire Alps.

We introduce, in a first step, the nivality index and use it for an operational definition of the ecotone. The nivality index, defined as the area ratio of nival and alpine plant vegetation, is exclusively based on plant characteristics (see formula (1)).

In a second step, we compare the nivality index with the snow duration (see formula (2)) measured at routine climate stations. By using standard linear analysis techniques, we consider both independent quantities as functions of altitude and time.

The key step is the third: we relate both nivality index and snow duration profiles to the mountain temperature; the mountain temperature replaces the familiar station temperature. For this purpose we adopt a nonlinear probabilistic model originally designed for winter snow duration [21]. The emerging state functions, separately analyzed for vegetation and snow, will exhibit a pronounced coincidence of their characteristics.

The methodical independence of the vegetation from the snow analysis is an important aspect of this study. While ecological textbook wisdom maintains that nival plants and summer snow are intimately related [3, 4] our present evaluation strategy treats the nivality index as strictly independent upon local snow observation; similarly, the snow cover will be gained from observations that are strictly independent of vegetation observations. The coincidence between the nivality index and snow cover that we shall find at the end will therefore be a robust result.

2. Materials and methods

2.1. The nivality index

We have measured over the years, as part of the GLORIA program [13, 14, 22], the plant cover in the alpine–nival ecotone of Mt Schrankogel (figures 1(b)–(d)). Implemented on the south-west slope of this mountain are 162 permanent square measuring plots with an area of $1 \times 1$ m each, referred to as quadrats [22]. In two field campaigns (1994, 2004), we recorded the area cover of 50 vascular plant species (see supplementary data available at stacks.iop.org/ERL/6/014013/mmedia, section 1, for the full species list and groupings, including measurement details) and combined these into a nival and an alpine group [14, 20, 22–24]. The six nival species are (the nomenclature follows [25, 26]): Androsace alpina, Cerastium uniflorum, Poa laxa, Ranunculus glacialis, Saxifraga bryoides, and Saxifraga oppositifolia. The distribution of these species has its center above the closed alpine grassland. They occur commonly on summits above 3300 m and form the plant assemblages of the nival zone that are characteristic throughout the siliceous Alps. The 44 alpine species include: Carex curvula, Oreochloa disticha, Silene acaulis, Minuartia sedoides, Festuca intercedens, and Agrostis rupestris.

Within a quadrat the areas of all nival and alpine species (figure 1(d)) are added together into $\Sigma_{niv}$ and $\Sigma_{alp}$, respectively. With these we define the mountain nivality index:

$$m = \frac{\Sigma_{niv}}{\Sigma_{niv} + \Sigma_{alp}}.$$  

$m$ is a number between 0 (‘only alpine species in the quadrat’) and 1 (‘only nival species’). Averaged over all quadrats, the nival plants, in 1994, covered 13.8% and the alpine plants 14.3% of the area, which implies that the quadrats are only partially covered with vegetation (about a quarter). These coverages changed in 2004 to 10.1% nival and 15.0% alpine. The total number of independent usable $m$-values is 308 (153 $m$-values in 1994 and 155 in 2004)\(^6\).

2.2. The snow duration

To relate the ecotone to snow [27], we take daily snow depth measurements from our Alpine data set 1975–2000 used earlier for winter and spring [21, 28–31], plus observations from Austria for 2001–2004, and use them for the summer seasons (JJA) 1975–2004. We count a day with snow cover below or above the threshold 2 cm [28] as $n = 0$ or 1. The average of this stochastic quantity (daily index $i = 1, \ldots, I$) yields the relative snow cover duration of this season:

$$n = \frac{1}{I} \sum_{i=1}^{I} n_i.$$  

$n$ is close to 0 at low stations for high temperatures (‘never snow’) and close to 1 at high stations for low temperatures

\(^6\) There are 324 measured $m$-values but 16 had to be skipped because of saturation (see section 2.2).
Figure 1. Schematic overview of data origins. (a) Routine climate stations in the Alps recording snow depth 1975–2004 (black dots): stations selected for present evaluation (orange dots); the location of Mt Schrankogel (47.04°N, 11.1°E, 3497 m) in Tyrol, Austria (green star). (b) Mt Schrankogel (5 September 2009, 13:15 UTC, from the south at a distance of about 2 km): the alpine zone is mostly snow-free, the nival zone is covered with snow, and the transition zone shows a typical patchwork pattern of snow-covered and snow-free areas. Field data collected in 1994 and 2004 on the south-west slope (orange ellipse) between 2900 and 3100 m. (c) Sketch of the theoretical concept of ‘ecotone isolines’. (d) Typical field quadrat with alpine (red polygons) and nival plants (yellow polygons) taken at altitude 3010 m, 31 August 1994.

(‘always snow’). The extreme values 0 and 1 have estimated error zero (corresponding formally to infinite accuracy). These saturated observations must be excluded from further processing (this applies also for \( m \)) because they cannot be used in a fit that is based on accuracy estimates for the cost function (compare formula (S14) in the supplementary data available at stacks.iop.org/ERL/6/014013/mmedia; see also Hantel and Maurer [32]). Of the 268 European climate stations originally available (dots in figure 1(a)) only 40 were eventually used (orange points in figure 1(a)) mainly because of the saturation criterion for \( n \) (for details see [32] and supplementary data available at stacks.iop.org/ERL/6/014013/mmedia, section 2.2). Not all stations report unsaturated snow data in each year of the 30 year period; the total number of usable \( n \)-values was represented by 664 station summers. \( n \), like \( m \), comes as a function of \( \theta \) (time) and \( z \) (altitude).

2.3. The central altitude

The ecotone comprises the entire transition zone and thus cannot be fully described by one single value of \( m \). Yet we find it useful for a number of purposes to identify the ecotone by picking one specific isoline of \( m \). Connecting in the horizontal direction different plots with \( m = \text{const.} \) at Schrankogel would generate ecotone isolines (schematically sketched in figure 1(c)). Out of the infinite number of such isolines we shall focus here on the median ecotone line \( m = 0.5 \) which seems to be the most natural choice. This virtual boundary is an idealized limit that separates the (lower located) area with mostly alpine plants from the (higher located) area with mostly nival plants; at \( m = 0.5 \) the cover of alpine and nival species is balanced. The geometrical position \( z \) of this boundary in a given summer will be referred to as the central altitude of the ecotone.

Similarly, the specific value \( n = 0.5 \) of the snow duration defines the median snowline; it is located at the central altitude \( H \). The concept of the median snowline has recently been elaborated on by Hantel and Maurer [32]. The idea is that the median snowline can be simply found from the observed snow duration. It is located where the probability of encountering snow in summer is 50%; this implies that at the same altitude the probability of encountering no snow would also be 50%.

We anticipate that the central altitudes \( Z \) and \( H \) will be dynamically related. One reason is that 7 weeks of summer snow cover (corresponding to \( n = 0.53 \) for JJA) is about the maximum that alpine species can stand [2].
The central altitude of the median ecotone line, averaged over the years 1994 and 2004, can be found by fitting a straight line through the measured \( m(\theta, z) \) and determining the altitude \( Z \) at which \( m = 0.5 \). In a similar manner, the central altitude \( H \) of the median snowline, averaged from 1975 to 2004, is determined linearly from the measured \( n(\theta, z) \).

2.4. Trend estimates of the nivality index and snow cover

At first glance, the trend of \( m \) cannot be determined because we have data for just two years (1994, 2004) which may indicate a time change at best but constitutes no trend. However, there are many plots in the vicinity of the central altitude that all show a relatively small but consistently negative time derivative:

\[
\frac{\Delta m(z)}{10 \text{ years}} = \frac{m(2004, z) - m(1994, z)}{2004 - 1994} \quad (3)
\]

for constant altitude \( z \). The method of pairwise slopes [33] now offers a possibility of estimating the time trend of the nivality index in the form of the median of the ratio (3), averaged over a proper number of independently measured time derivatives \( \Delta m(z)/(10 \text{ years}) \) at different quadrats located at altitudes \( z \). We shall provide not only the median but also the full pdf of the corresponding frequency distribution.

For the time change of \( n \) we will apply the same method. The median of the frequency distribution of

\[
\frac{\Delta n(z)}{\Delta \theta} = \frac{n(\theta_2, z) - n(\theta_1, z)}{\theta_2 - \theta_1} \quad (4)
\]

will be an estimate of the linear time trend of the snow duration. Formulas (3) and (4) are conceptually equal, but there is a conspicuous difference in data availability of \( m \) and \( n \). The method of pairwise slopes uses all independently measured data in a time series for calculating ‘time slopes’ according to formula (4). If there are \( k \) time instants there are \( k(k - 1)/2 \) different time slopes in (4). For \( k = 2 \) this yields just one, and this is the situation in formula (3). However, for the snow data \( n \), as opposed to the vegetation data \( m \), we have up to \( k = 30 \) different observation years at one climate station during the observation period 1975–2004 yielding up to 435 different time derivatives for this station located at altitude \( z \).

A further task is to decide which altitude interval is to be allowed to contribute to the median. In the most ideal case the data should only be taken from plots located at the central altitude. However, this would severely limit the available data; thus we will be forced to take data from a considerably larger interval.

Taken together, these conventions yield a total of 140 nivality trend and 1810 snow trend data (see figure 3 below).

2.5. The mountain temperature

The dimensionless ratios \( m \) and \( n \) are formally similar; we attempt to analyze them using the same theoretical concept. For this we use a nonlinear probabilistic model [21, 28] developed recently for winter snow cover. The model interprets \( n \) as the probability \( \Phi \) that water is frozen. \( \Phi \) depends on the mean and variance of the station temperature \( t \).

We shall nevertheless not use \( t \) in our probabilistic model because \( t \) is influenced by two independent mechanisms: the climate-scale surface temperature \( T \) and the contribution of local-scale temperature that depends linearly on the altitude \( z \). Both mechanisms are mixed in \( t \) and cannot be distinguished.

In order to explicitly separate the two effects we introduce (see supplementary data available at stacks.iop.org/ERL/6/014013/mmedia, figure S2) the mountain temperature as follows

\[
\tau = T + cz; \quad (5)
\]

\( \tau \) combines the large-scale European effect described by \( T \) with the small-scale vertical lapse rate effect due to \( z \). The parameter \( c \) in the definition (5) is the vertical temperature gradient; it will not be specified externally but determined from the data fit. \( \tau \) replaces \( t \); it is the independent argument for the state function to be defined farther below. \( T \) is obtained from the monthly gridded CRU temperatures [34], with resolution half a degree in latitude and longitude, averaged horizontally over Europe [28] and time averaged over each of the summers 1975–2004. We use this European temperature \( T \) for the \( n \)-data (a total of 30 \( T \)-values, one for each summer of the record).

There is a secondary reason for introducing \( \tau \): station temperature is not available in our ecotone data set. Thus it is of practical importance that \( t \) can be replaced by the mountain temperature.

Other parameters like local aspect ratio or slope may also have an influence on \( \tau \). Yet we believe that their impact at Schrankogel is low because our plots are located in uniform terrain at the south-west face of the study mountain (see figure 1). As to the snow stations, the impact of local-scale aspect and slope is presumably stochastic. What is not stochastic is the dependence on latitude and longitude. We have studied this latter effect for the Alpine snow cover [32] and found that it is not very big. Here we prefer to skip it in order to have optimal consistency with the Schrankogel vegetation data.

2.6. The prior period concept

Despite their formal similarity, the ratios \( m, n \) cannot be naively compared since there is a basic difference between them due to lifetime: snow is generated from zero every year while vegetation has a lifetime of many years. This implies that the snow cover is in approximate balance with the seasonal environmental conditions of the actual year as expressed by \( T \), whereas the nivality index has something like a ‘memory’ of the conditions of earlier years; it follows that \( m \) cannot normally be in balance with \( T \) of the actual year.

As to the length of this memory we empirically decided, after some numerical experimentation, that 20 years is an acceptable first choice. We arbitrarily introduce the concept of a prior period as the preceding 20 year period that impacts the nivality index in 1994; thus, 1975–1994 will be referred to as

\footnote{In the original studies [21, 28] we had introduced Alpine mountain temperature for \( \tau \); here we switch to mountain temperature for greater generality.}
Yet we suggest that the nivality index \( m \) parameters \( \tau \) one for each station summer.

functions. \( Z \) snow; they follow as fitted quantities of the respective state ecological factor (e.g., \([3, 4]\)).

assumption that, at the level of the present model, all these act together as stochastic noise while temperature is the leading assumption.

The parameters \( \tau \) are defined above as the probability that water is frozen. \( N \) was defined above as the probability that water is frozen.

A caveat may be added here. Besides temperature there may be other influential processes like precipitation, wind, radiation, and others that are not considered in our functional dependence of \( m \).

We implement this by replacing \( N \) through \( M \) in (6). The state curves \( M(\tau) \), \( N(\tau) \) interpolate measured values of \( m \), \( n \), respectively. We distinguish between \( M \) and \( N \), if necessary, by adding subscripts \( m \), \( n \) to the fitted parameters \( s_0 \), \( \tau_0 \), \( c \).

A caveat may be added here. Besides temperature there may be other influential processes like precipitation, wind, radiation, and others that are not considered in our functional dependence of \( m \).

Yet our results are consistent with the assumption that, at the level of the present model, all these act together as stochastic noise while temperature is the leading ecological factor (e.g., \([3, 4]\)).

The central altitudes are implicitly defined through the state function by setting \( z = Z \) in (5) for the median ecotone line and \( z = H \) for the median snowline; solving for \( Z \) and \( H \), plus observing the condition \( M(\tau_{0,m}) = \Phi(0) = 0.5 \) for the ecotone and \( N(\tau_{0,n}) = \Phi(0) = 0.5 \) for the snowline, yields

\[
Z = \frac{\tau_{0,m} - T_{\text{prior}}}{\epsilon_m}, \quad H = \frac{\tau_{0,n} - T}{\epsilon_n}.
\]

The parameters \( \tau_0 \), \( c \) are of course different for ecotone and snow; they follow as fitted quantities of the respective state functions. \( Z \) can only be defined with \( T_{\text{prior}} \). \( H \), on the other hand, is for the actual year to be calculated with \( T \) for the same year; for the prior period it is to be calculated with \( T = T_{\text{prior}} \) (necessary below in figure 4(c) for comparing the sensitivity profiles of vegetation and snow).

2.8. Sensitivity profiles of nivality and snow

The significance of the central altitudes \( Z \) and \( H \) can now be judged by considering the \( \tau \)-slope of the state curves. We call the vertical profile \( s(\tau) \) of the \( \tau \)-slope the sensitivity profile\(^8\); it is the \( \tau \)-derivative of the model function (6), applied to both \( M \) and \( N \), and is negative throughout (supplementary data available at stacks.iop.org/ERL/6/014013/mmedia, formula [SS5]).

The extremum \( s_0 \) of \( s \) is adopted at \( \tau = \tau_0 \); this argument of \( \Phi \) yields \( M = 0.5, N = 0.5 \), which is the condition for the central altitudes. For all other values of \( \tau \), both above and below the central altitudes, the sensitivity \( s(\tau) \) is absolutely smaller than \([s_0]\). It is this property of the central altitudes \( Z, H \) that a posteriori justifies our above choice of the median ecotone line located at \( m = 0.5 \) and median snowline located at \( n = 0.5 \).

The state function \( M(\tau) \) and the sensitivity function \( s_m(\tau) \) describe the observed nivality index data set equally well. However, \( s_m(\tau) \) is more revealing and thus we consider \( s_m(\tau) \) simply as the ecotone function. Similarly, we consider the snow function \( s_n(\tau) \), the derivative of the state function \( N(\tau) \), as the relevant description of the observed snow duration profile. Comparing the two sensitivity profiles \( s_m(\tau), s_n(\tau) \) with each other will yield the main result of this study.

2.9. The trend of the central altitudes

The central altitude \( Z \) of the ecotone is the average over the two observation years 1994, 2004; it is given, along with the central altitude \( H \) of the snow, by formula (7). In order to obtain an estimate for the trend of \( Z \) in this time interval (as well as for the trend of \( H \) in the interval 1975–2004) we proceed as follows.

The nivality index \( m(\theta, z) \) is a function of time \( \theta \) and, for given \( \theta \), a monotonic function of altitude \( z \). Thus \( z(\theta, m) \) is also a monotonic function of \( m \). Now the time change of \( z \) for constant \( m \) can, by means of an elementary formula of analysis, be written as

\[
\frac{\partial z(\theta, m)}{\partial \theta} = -\frac{\partial m(\theta, z)/\partial \theta}{\partial m(\theta, z)/\partial z}.
\]

An appropriate estimate for the numerator of (8) is the median trend \( \Delta m/\Delta \theta \). As regards the denominator, the vertical gradient of the state function \( M(\tau[T(\theta), z]) \) in a given year \( \theta \) would read (observing the chain rule of analysis at the central altitude \( Z \))

\[
\frac{\partial M}{\partial z} = \frac{\partial M(\tau)}{\partial z} \frac{\partial z}{\partial z} = s_{0,m}e_m.
\]

Thus by combining the observed trend of \( m \) with the analyzed parameters \( s_{0,m}, e_m \) from the nonlinear fit, the trend of \( Z \)

---

\(^8\) Following climatological parlance, we use the following nomenclature: the sensitivity of a climate function is its derivative with respect to large-scale temperature; the trend is its derivative with respect to time.
For the two years 1994 (153 unsaturated observations used) and 2004 crosses summer (Jun/Jul/Aug) for the period 1975–2004; the regression line \( z \) versus altitude \( s \) slopes. Both substeps will be made with linear techniques; we

\[
\begin{align*}
\mu &= \frac{1}{s_{0,m} c_m} \left[ \frac{\partial n(\theta, z)}{\partial \theta} \right]_{z=Z}.
\end{align*}
\]

An attractive aspect of this method is that no trend estimate of the observed climate temperature \( T \) is required. In fact, only the measured nivality index, including its time change, is taken as a basis for the trend estimate of the central altitude \( Z \).

The equivalent approach can be applied for estimating the trend of the central altitude \( H \) of the snow duration \( n(\theta, z) \) with the result

\[
\begin{align*}
\frac{dH(\theta)}{d\theta} &= -\frac{1}{s_{0,n} c_n} \left[ \frac{\partial n(\theta, z)}{\partial \theta} \right]_{z=H}.
\end{align*}
\]

We shall apply these formulas below.

3. Results

Of the three steps that have been sketched in section 1, the first has been achieved above by introducing the nivality index \( m \), in parallel to the snow duration \( n \). The second step will be to compare the observed \( m \) at Schrankogel with \( n \) measured at climate stations across the Alps. Since the data for both ratios come as functions of time \( \theta \) and altitude \( z \) there are two substeps: compare the time-mean profiles \( m(z) \), \( n(z) \) through linear regression analysis; and compare the time trends of \( m(\theta) \), \( n(\theta) \) with each other through the method of pairwise slopes. Both substeps will be made with linear techniques; we consider this approach as preliminary. The third, and main, step will be the nonlinear analysis of the data \( m(\theta, z) \) yielding the state function \( M(\tau) \) and the ecotone function \( s_m(\tau) \), and similarly the analysis of the data \( n(\theta, z) \) yielding the state function \( N(\tau) \) and the snow function \( s_n(\tau) \).

3.1. Linear analysis with respect to altitude

Standard linear analysis of the Schrankogel data (figure 2(a)) and the Alpine snow data (figure 2(b)) describes the altitude dependence of \( m \) and \( n \), irrespective of time; this yields the regression lines \( R^2 = \text{explained variance})

\[
\begin{align*}
m(z) &= 2.48(\pm 0.30)(z/\text{km}) - 6.88(\pm 0.89); & R^2 &= 0.19 \\
n(z) &= 0.41(\pm 0.02)(z/\text{km}) - 0.68(\pm 0.04); & R^2 &= 0.44
\end{align*}
\]

We use these formulas to determine the central altitudes at which the median values \( m = 0.5, n = 0.5 \) are adopted. This yields \( Z = (2977 \pm 5) \) m for the vegetation and \( H = (2911 \pm 40) \) m for the snow\(^9\).

\(^9\) Errors in this study are given as 1 \( \sigma \).
3.2. Linear analysis with respect to time

Figure 3(a) presents the frequency distribution of the observed 10 year trend estimates \(\Delta \frac{m}{\Delta \theta}\) at 140 quadrats in the vicinity of \(Z\), the altitude of the median ecotone line. Anticipating the halfwidth \(D_m\) of the ecotone function to be developed in the nonlinear analysis below, we have taken the data from the quadrats within the 214 m broad altitude band \(Z \pm D_m/2\). This yields the median of the time change in the belt of the ecotone that is most sensitive with respect to temperature (sensitivity \(s_m\) between \(s_{0,m}\) and \(s_{0,m}/2\); see the green curves in figure 4(c) below). Equivalently, figure 3(b) presents the frequency distribution of the observed 10 year trend estimates \(\Delta \frac{n}{\Delta \theta}\) for the snow duration in the vicinity of \(H\), the altitude of the median snowline. The vertical width of this 992 m broad band has been chosen as \(H \pm D_n/2\). This is a compromise between having enough data and staying sufficiently close to the central altitude. For this reason figure 3 will somewhat underestimate the median trends.

The curves of figure 3 yield the following trend estimates:

\[
\frac{\Delta m}{\Delta \theta} = -(0.090 \pm 0.092)/10 \text{ years}; \\
\frac{\Delta n}{\Delta \theta} = -(0.136 \pm 0.184)/10 \text{ years}. \\
\tag{14}
\]

The uncertainties given represent one standard deviation so the estimates (14) are not at all significant. Yet they yield valuable information for the parallel reduction of the nivality index and the snow duration under climate change. The trend of the snow duration is somewhat stronger than that of the nivality index, which is to be expected.

3.3. Nonlinear probabilistic model analysis: the state functions

The state function \(M(\tau)\) interpolates measured values of \(m\) (figure 4(a)). The curve parameters \(s_{0,m}, t_{0,m}, c_m\) are listed in figure 5. For the central altitude of the ecotone, \(M(\tau)\) yields \(Z = (2967 \pm 16)\) m (see also supplementary data available at stacks.iop.org/ERL/6/014013/mmedia, table S6), indistinguishable from \(Z\) found from linear regression.

The state function \(N(\tau)\) for \(n\) is drawn in figure 4(b); curve parameters \(s_{0,n}, t_{0,n}, c_n\) appear in figure 5. For the central altitude of the snowline we find \(H = (2897 \pm 140)\) m (see also supplementary data available at stacks.iop.org/ERL/6/014013/mmedia, table S6), indistinguishable from \(H\) found from linear regression.

The physical significance of the fitted parameters (listed in figure 5) is as follows: \(s_p\), a negative quantity, is the extreme value of the sensitivity profiles; this parameter

10 Errors of the fitted parameters are given as \(1\sigma\), determined with the bootstrap method [36] using 2000 runs.

Figure 4. State curves for the nivality index and snow duration (Jun/Jul/Aug). (a) \(M(\tau)\) for \(m\) at Mt Schrankogel (years 1994 and 2004). The shading captures 68% of the data points (corresponding to \(1\sigma\) in the \(y\)-direction); the shading does not show the accuracy of the fitted state curve. (b) As (a) but for state curve \(N(\tau)\), applied to \(n\) at climate stations across the Alps (threshold 2 cm, all years 1975–2004). (c) Sensitivity profiles of state curves as a function of the altitude. Profiles of \(M(\tau)\) are green, those of \(N(\tau)\), blue. Profiles are projected to the temperature of prior’94 (dashed curves) and prior’04 (solid curves).
**Figure 5.** Summary of the concept and main findings of this study. Errors are only given for parameters of state curves; errors of derived quantities are cited in the text.
consistently negative (i.e., the corresponding temperature gradient is correctly directed downward). This proves that both vegetation data and snow data implicitly carry temperature information, consistent with our basic modeling hypothesis. \( r_0 \) is a reference parameter in the fit with no obvious physical significance.

The sensitivity profiles \( s_m(\tau) \) for \( M(\tau) \) and \( s_n(\tau) \) for \( N(\tau) \) are drawn in figure 4(c) as a function of \( z \). The snow function \( s_n(\tau) \) represents the stochasticity which is realized as the fluctuation of snow cover from year to year, extreme at the altitude of the median snowline. Both the ecotone function \( s_m(\tau) \) and the snow function \( s_n(\tau) \) peak between about 2900 and 3000 m at their respective central altitudes \( Z \), \( H \) and both move slowly upward from \( T_{\text{prior}94} \) to \( T_{\text{prior}04} \) (dashed and solid curves in figure 4(c); the trend is discussed in section 4).

The coincidence between the parameters \( Z \) and \( H \) quantifies how well the ecotone function is embedded into the snow function. This coincidence is the main result of our study; it is a robust result because all vegetation plots of the measurement campaign at Schrankogel happened to sit right in the center of the snow profile of the Alps. This observation may be accidental; the ecotone function at a mountain different from Mt Schrankogel might be located off the center of the snow function valid for the Alps. However there are no data available at present so this problem must be left for later research.

The fitted parameters of the state functions and the quantities derived from them can be discussed from various perspectives. In the following we focus briefly upon their response with respect to temperature (sensitivities) and with respect to time (trends).

### 3.4. Sensitivity parameters

There are three sensitivity quantities listed in figure 5. First, there is the parameter \( s_0 \), referred to as the extreme sensitivity of state curves. Second, the entire sensitivity profiles: the ecotone function \( s_m(\tau) \), and the snow function \( s_n(\tau) \); the parameters \( s_{0,m} \), \( s_{0,n} \) are just the extreme values of the sensitivity profiles. Third, the temperature sensitivity of the central altitude; the latter quantity is the \( T \)-derivative of the central altitude of the respective median line as determined from equation (7):

\[
\frac{dZ}{dT_{\text{prior}}} = -\frac{1}{c_m}; \quad \frac{dH}{dT} = -\frac{1}{c_n}. \quad (15)
\]

It yields the sensitivities of \( Z \) and \( H \) to European temperature \( T \) and is given by the inverse of the fitted temperature lapse rates. The result of equation (15) is valid for the entire observation period. Also listed in figure 5 are the halfwidths of the sensitivity profiles. \( D_m = (214 \pm 129) \text{ m} \) represents the halfwidth of the sharply defined ecotone while \( D_n = (992 \pm 153) \text{ m} \) stands for the much broader snow profile across the Alps.

### 3.5. Trend parameters

Time trend information of this study is condensed in figure 3. The pdfs of the trend estimates of the nivality index and of the snow duration have been gained with the method of pairwise slopes [33] as discussed above in section 2. The result, expressed in equation (14), can be interpreted as follows. For example, \( \Delta m / \Delta \theta = -0.090/10 \text{ years} \), when applied at the median snowline \( z = Z = 2967 \text{ m} \), would imply that the nivality index \( m \) at this altitude has been reduced from 0.50 in 1994 to 0.41 in 2004. This reduction would be much smaller at higher levels. As to snow, \( \Delta n / \Delta \theta = -0.136/10 \text{ years} \), when applied at the median snowline \( z = H = 2897 \text{ m} \), would imply that the snow duration \( n \) at this altitude has been reduced from 0.50 to 0.36 in ten years. This reduction would also be smaller at higher levels.

Further, inserting the estimates (14) into equations (10) and (11) we find

\[
\frac{\Delta Z}{\Delta \theta} = -\frac{\Delta m / \Delta \theta}{s_{0,m} c_m} = (20.0 \pm 27) \frac{m}{10 \text{ years}} \quad (16)
\]

\[
\frac{\Delta H}{\Delta \theta} = -\frac{\Delta n / \Delta \theta}{s_{0,n} c_n} = (142 \pm 193) \frac{m}{10 \text{ years}}. \quad (17)
\]

These trend estimates are not significant. Yet they can be interpreted in the sense that the ecotone line moves upward, presumably under the influence of the upward moving snow cover. The trend of the snow cover is considerably stronger; this reflects the fact that snow cover reacts instantaneously to climate change whereas the vegetation has a longer memory. The longevity of high mountain species causes strong inertia, influenced not only by the actual year but also by earlier years. This suggests that the nivality index which may have been in balance with the snow under stationary climate conditions runs out of balance when climate change sets in. However, these implications are largely speculative at present because the data accuracy is not yet sufficient.

### 4. Discussion

We have shown in this study that the altitude interval characteristic for the alpine–nival ecotone at Mt Schrankogel happens to sit right in the center of the snow profile across the entire Alps. The rigorously analyzed ecotone profile in figure 4(c) is located entirely within the snow profile.

Standard regression and frequency analysis of the original field data (figures 2 and 3) can only show that the nivality index \( m(\theta, z) \) increases with altitude \( z \) and gently decreases with time \( \theta \); this traditional evaluation technique does not provide a dynamical explanation. The added value of our present nonlinear probabilistic model (schematically summarized in figure 5) is that the entire information of the observed \( m(\theta, z) \) becomes condensed, with the mountain temperature \( \tau \), into state function \( M(\tau) \) and ecotone function \( s_m(\tau) \); the equivalent concentration is reached by \( N(\tau) \) and \( s_n(\tau) \) which fits the observed snow duration data \( n(\theta, z) \). A prominent result is that the sensitivity profiles coincide at the central altitudes \( Z \), \( H \) of the two curves (figure 4(c)). The state curves are time independent; yet the gentle upward shift of the sensitivity profiles from prior’94 to prior’04 seen in figure 4(c) follows from the parameters of \( M \) and \( N \) since the time dependence is implicit in \( \tau \) through \( T(\theta) \).
The central altitude of the snow profile varies somewhat with the specific choice of the season, in our case JJA. The choice of this temporal window for the evaluation of the snow data is justified as follows: Gottfried et al [2] have shown that snow melt takes place from early June until July around the alpine–nival ecotone at Mt Schrankogel. The earlier part of the growing season is the most decisive time for plant growth and reproduction while the time of winter onset (usually during September at Mt Schrankogel) is far less important [3]; therefore we excluded September from the snow analysis.

From the ecological perspective it remains to be asked how the approximate equilibrium process hypothesized here for the nival index can be acceptable [35]. Stochasticity of the snow regime, understood as variance of the snow cover, and realized as unpredictability by the vegetation, peaks at the alpine–nival ecotone; this is consistent with the theoretical concept of ecotones as ‘environmentally stochastic stress zones’ [12].

Note that Van der Maarel [12] referred to ecotones in the sense of temporal fluctuation zones and termed boundaries that are structured by spatial gradients as ecoclines. The alpine–nival boundary shows both features: spatial gradients of (mean) temperatures, soil and substrate properties and vegetation patterns; and a temporal highly variable summer snow regime. Therefore we see justification for using the wider term ecotone. The fluctuating snow regime triggers counteracting processes which hold the central altitude Z of the ecotone in balance.

Early snow melt in spring and late snow in autumn improve reproductive success [37, 38] but may also mean increased exposure to lethal frosts in the early and late seasons [5, 9, 39, 40]. Snow protection may thus be essential since even in mid-summer cold spells occur regularly, which affects plants with low frost tolerance [39, 41]. Snow, on the other hand, may interrupt seed production [38].

These elementary processes influence nival and alpine plants differently. Both groups can be distinguished not only by their altitudinal distribution centers [20, 23, 24] but also by their climatic niches. Nival plants are highly snow tolerant [2]. They maintain viable populations at snow rich sites; a typical example is that of Ranunculus glacialis which survives even one or two years of permanent snow pack [42]. Alpine plants, on the other hand, are known to prefer sites with less summer snow and warmer temperatures [2]. This favors, in the present climate warming stage, the more competitive alpine species over the nivals; typical examples are Silene acaulis and Oreochloa disticha which expanded at Mt Schrankogel mostly at the cost of Androsace alpina, 2nd Saxifraga bryoideas and Cerastium uniflorum [22]. In the longer term the alpines tend to outcompete the nival plants during warm periods; the opposite happens during cold periods.

It appears that the alpine–nival ecotone is exactly at the place where these processes are in a state of dynamic equilibrium. This interpretation applies to the ecotone for both stationary and changing climate conditions. We conclude that the vegetation data m can indeed be evaluated with our probabilistic model and in this sense pass the test required above.

Figure 4(c) suggests that the ecotone profile moves upward under climate warming [43–45]. The trend reported elsewhere for the various vegetation zones worldwide is in the range 60–200 m per century [22, 46, 47]. Assuming this figure as the zeroth estimate for the globe with an estimated 0.74 °C centennial warming trend [48] we expect an order of magnitude temperature sensitivity of 81–270 m °C−1. This figure can be contrasted with our sensitivity results ΔZ/ΔT ≈ (47 ± 36) m °C−1 for the ecotone at Mt Schrankogel and ΔH/ΔT ≈ (346 ± 48) m °C−1 for the summer snow profile at Alpine climate stations.

Our finding that the ecotone in figure 4(c) tends to follow the snow fluctuations is in accord with general ecological knowledge [3, 4]. Yet our estimates for the trends of the ecotone and the snow profile given in equations (16) and (17) are quite different; further, both have a large scatter. Thus they should be compared with caution. After all, our present analysis is the utmost one can press out of vegetation data from just one Alpine summit available, combined with a limited number of stations that report summer snow.

Despite being derived from a case study, the methodical framework presented here offers perspectives for application to other—bioclimatically similar—mountain systems. Another implication is biodiversity: as the extent of the nival zone is restricted by the upper elevation limit of mountain ranges, the ongoing shrinking of this belt may have considerable consequences for mountain biodiversity [49–52]. Thus the coincidence between vegetation and snow, as we have tried to quantify here, may shed new light on the mechanisms that govern vegetation and vegetation changes at the limits of plant life.

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