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**A comparison between different treeline types shows contrasting responses to climate fluctuations**

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## Abstract

Treeline position is mainly determined by growth season temperature, but the response of treelines to climate warming is not uniform worldwide. We compared treeline structure, dynamics and thermal profile in nearby areas with different treeline type, species composition and bioclimatic conditions.

We performed a detailed survey of different treeline types in three areas of Italian Alps and Northern Apennines. Every tree individual was recorded along altitudinal transects from the closed forest to the species limit. Treeline structure and dynamics were described through altitudinal limits of tree height, density and age. Data were elaborated by principal components analysis. Temperature regime of the three sites was assessed from homogeneous historical climatic data.

Treeline was different in the three areas for species composition, shape and dynamics. Both Alpine sites showed diffuse treeline, but only one showed advancing dynamics. Apennine treeline was abrupt and static, with higher temperature at the tree limit.

Our study showed the variable dynamics of treelines within a relatively restricted area and the connection between treeline shape and dynamics. An important role is played by species composition, determined by bioclimatic and historical features. **These factors should be taken into account when modelling future treeline dynamics at global scale.**

**Key words:** Alps; Apennines; *Fagus sylvatica*; *Larix decidua*; *Pinus cembra*; Temperature; Treeline dynamics

## Introduction

The position of the treeline (the uppermost or northernmost limit of tree growth form) represents a well-known climatic boundary, and a powerful proxy for past and present climate variations.

Growth season temperatures are widely considered the main factor affecting the position of both latitudinal and altitudinal treelines (Tranquillini 1979; Körner 1998; Körner & Paulsen 2004; Körner & Hoch 2006); however, also the role of winter temperatures and of precipitation regimes has proved to be critical (Jobbagy & Jackson 2000; Camarero & Gutierrez 2004; Bader et al. 2007; Caccianiga et al. 2008; Harsch et al. 2009; Kharuk et al. 2010). **Körner (1998, 2008) and Körner and Paulsen (2004) found constant mean ground temperature values of the growth season at the treeline worldwide. These values were set equal to  $6.7 \pm 0.8$  °C by Körner & Hoch (2006). Successive statistical modelling confirmed data from in situ measurements suggesting a minimum growth season temperature of 6.4°C globally (Paulsen & Körner, 2014).** Only in few cases (e.g. *Fagus sylvatica* Mediterranean treelines) temperatures at the treeline were found to be substantially higher, phenomenon interpreted as due to genus-specific boundaries (Körner and Paulsen 2004).

However, the ongoing global temperature increase is not causing a global advance of treelines worldwide (Holtmeier & Broll 2007; Batllori et al. 2009; Harsch et al. 2009; Harsch & Bader 2011) thus emphasizing the complexity of climate-treeline relationship; moreover, the different species composition at the treeline (driven by bioclimatic, historical or biogeographic factors) could result in different responses to climatic forcing (Lloyd et al. 2005; Caccianiga & Payette 2006).

Studies combining detailed analysis at local or regional scale (e.g. Wiegand et al. 2006; Danby & Hik 2007; Bader et al. 2007) or based on global meta-analysis (Harsch et al, 2009; Harsch & Bader 2011) showed a relationship between treeline type and its response to climate variations, and thus its importance for the inference of the underlying processes. To this purpose, treelines could be classified as “abrupt” (i.e. a continuous canopy with no decreasing tree density and height right up

to treeline), “diffuse” (characterized by decreasing tree density with increasing altitude or latitude) or “krummholtz” treelines, characterized by stunted trees (Wiegand et al. 2006; Harsch et al. 2009; Harsch & Bader 2011).

The assessment of treeline responses to climate is strongly influenced by the spatial and temporal scale of the analysis (Holtmeier & Broll 2005). At local scale local factors can override general climatic trends and comparisons between different situations are often not possible; on the other hand, regional to global scale analyses must rely on data of different origin and homogeneity or on wide remote sensing data set which may not allow a comparison of the actual site conditions.

The present work aims to compare treeline dynamics in areas with different treeline type, species composition and bioclimatic conditions applying a homogeneous and detailed, individual-based analysis. Our hypotheses are: 1) different treeline types exhibit different age structure and dynamic behaviour; 2) temperatures at the tree limit are similar among the different sites.

We included areas as close as possible within the same biogeographic region, which agree (Alps) or not (Apennines) with the general scheme of temperature distribution at the treeline assessed worldwide by Körner and Paulsen (2004). We chose sites where climatic and paleoenvironmental data are available or under investigation, to outline any evidence of past treeline fluctuations occurred earlier than the present warming cycle, in order to assess long-time treeline dynamics. Finally, we compared the thermal profiles of the studied areas between them and with those reported in literature. We did not compare rainfall and snow permanence data because **of their lower availability and difficult extrapolation along altitudinal gradients**; in general, temperature is supposed to be the key factor globally driving treeline position (Körner and Paulsen 2004) and thus the most suitable parameter to be used to characterize treeline climatic condition of an area.

In the present work, the term "treeline" indicates generically the whole ecotone from the forest to the species limit. To indicate the limit of the tree growth form (i.e. the line connecting patches of uppermost undisturbed trees with individuals >3m in height; Körner & Paulsen 2004; Körner 2012) the term "tree limit" was used.

## Methods

### Study areas

The sampling was performed in three study areas, two on the Italian Alps (Valtellina and Val Camonica) and one on the Northern Apennines (Mt. Cusna) (Fig. 1). Study areas were chosen along a climatic gradient from continental to oceanic climate within the temperate bioclimatic region on the basis of the co-occurrence the following criteria. 1) The occurrence of natural treelines, i.e. treelines not affected as much as possible by human disturbance. To assess whether a treeline is "natural" or not, we used the criteria defined by Körner and Paulsen (2004): the consistent highest position of tree stands in a region and the visible decrease of maximum tree stature (not applicable in case of abrupt treeline), as well as the observation of plant communities and of the pattern of present human exploitation (grazing). 2) The different treeline shape. 3) The availability of climate data from nearby weather stations. 4) The occurrence of palaeoclimatic archives (i.e. bogs, paleosols, archaeological sites) in order to have the opportunity to put the observed present treeline dynamics in a wider temporal frame. All the sites lie within National Parks (Valtellina and Valcamonica: Stelvio National Park; Mt. Cusna: Appennino Tosco-Emiliano National Park). Valtellina site is located in the uppermost part of the valley. The climate is continental: precipitations are low ( $855 \text{ mm y}^{-1}$  at 1730 m a.s.l) and concentrated in summer. A closed forest dominated by *Picea abies* and *Pinus cembra* is replaced above c. 2200 m a.s.l. by open *Larix decidua* -*Pinus cembra* stands. Three transects were placed in this area (Table 1)

Val Camonica is separated by Valtellina by the Gavia Pass (2621 m); its climate is more humid (1410 mm y<sup>-1</sup> at 1820 m a.s.l.) and oceanic than that of upper Valtellina because of the north-south orientation of the main valley. *Pinus cembra* is very rare and sparse in the whole valley and absent in its uppermost part; coniferous woods are represented by closed *Picea abies*-dominated forests replaced by *Larix decidua* open forests above c. 2000 m a.s.l. Three transects were placed in this area (Table 1); although no important present disturbance could be detected, one of the transects (VC2) showed old artefacts (World War I trenches) in its uppermost part.

Mt. Cusna (2120 m) is the second highest peak of the Tuscan-Emilian Apennines, c. 230 km apart from the alpine sites. The climate is characterized by abundant and well distributed precipitations (2000 mm y<sup>-1</sup> at 1220 m a.s.l.), with summer minimum. The present vegetation is characterized by deciduous forest dominated by beech (*Fagus sylvatica*). *Abies alba* locally occurs; *Picea abies* is represented on the whole Apennine chain by two small relict populations (Ravazzi et al. 2006; Vescovi et al. 2010a,b), one of which c. 10 km apart from the study area. Five transects were placed in this area (Table 1).

#### Field work

The analysis was performed along altitudinal transect ranging from the closed forest to the uppermost individual of tree species, i.e. across the forest- and tree limit up to the species limit.

Up to the uppermost upright individual > 3 m, each transect was composed by 20x20 m quadrats; the total length of each transect was highly variable, depending from the overall structure of the treeline. (Table 1): altitudinal spacing between each quadrat was set at 1/10 of the total altitudinal range of the transect, i.e. from 10 m (Mt. Cusna) to 40 m (Valtellina).

Above the uppermost tree >3 m, every single individual was recorded following a linear transect 20 m wide up to the species limit.



Every living or dead individual belonging to a tree species occurring in the sampling sites was recorded and described (height, basal diameter, growth form, polycormy); its position was recorded through a portable GPS (Garmin GPSMap 60cx) with a precision < 6m. The minimum age of each individual was obtained by a core extracted with an increment borer as close as possible to the ground. For the individuals too small to be cored, the age was obtained through the counting of whorls (for conifers) and of scars separating each annual growth (for broad-leaved species and for *Larix decidua*) (Caccianiga & Compostella, 2011). For multi-stemmed individuals (particularly *Fagus sylvatica*) we sampled the oldest available stem; in this case, the minimum age obtained could be substantially lower than the actual age of the genet.

The altitude of the species limit was obtained from field data; that of the tree limit was obtained considering a wider area than that of the transects, including surrounding patches of uppermost undisturbed trees with individuals >3m; field data were then integrated with aerial photos and land use maps.

#### Temperature data

To assess the thermal profile of the study areas we calculated the altitudinal temperature gradient from thirty-year averaged monthly temperature data from all the nearest available weather stations (period 1961-1990 for Mt. Cusna, 1955-1984 for Val Camonica, 1955-1998 for Valtellina: Table 2). For each study area the responses of monthly temperature data to altitude were assessed through linear regression.

The obtained altitudinal gradients were used to calculate the average growth season temperature at the tree limit. Growth season was defined as the period with weekly mean air temperatures above zero, equivalent of 3.2°C at 10 cm soil depth (Körner & Paulsen 2004). As a comparison, we also considered the period of daily temperatures >0.9° C, following Paulsen & Körner 2014. Weekly and

daily means were calculated from one station per site where daily maximum and minimum data were available (Table 2). In order to have fully comparable data from the three areas we discarded years where data were incomplete for at least one station, comparing exactly the same years for the three sites; weekly and daily mean temperatures were thus calculated on 18 years within the interval 1973-2009.

Within this dataset further climatic indices were calculated for the present treeline: Kira's warmth index (WI), Holdridge's annual biotemperature (ABT) as indicators of growing season warmth, Kira's coldness index (CI) as indicator of coldness sum and Gorcynsky's continentality index (K); such indices were calculated following Fang and Lechowicz (2006); continentality index compensated for altitude (Icc: Rivas-Martinez 2004; Caccianiga et al. 2008) was also calculated.

## Analyses

Cores were mounted and prepared through the standard methods of dendrochronology and were visually crossdated through the occurrence of exceptionally narrow or large rings. The number of missing rings for off-centre cores was estimated locating the pith from the curvature of the inner ring and using the average growth rate of the contiguous ring (five, if available) (Paulsen et al. 2000; Batllori & Gutierrez 2008). Tree density was calculated as the number of individuals  $\text{ha}^{-1}$ . For *Fagus sylvatica* we considered the number of genets (stumps); the actual number of stems is higher, as individuals were often multi-stemmed. The age and dimensional structure of the treeline was assessed through the abruptness index proposed by Wiegand et al. (2006), calculated for tree age, height and density at the species limit, i.e. between the uppermost tree population and the treeless tundra.

In order to outline the main gradients within our dataset and to compare the different transects, principal components analysis (PCA) was applied using selected transect attributes: altitude of tree-

and species limit, distance (i.e. altitudinal difference) between them, maximum density, abruptness values at the species limit, mean age of the uppermost individuals (i.e. those recorded the altitudinal 90<sup>th</sup> percentile).

Finally, to compare the dynamic behaviour of the investigated treelines, the age structure of each quadrat was assessed calculating the distribution of individuals into 10-year age classes; afterwards, the age structures of all the quadrats were compared through Principal Component Analysis.

## Results

### *Altitudinal limits and treeline spatial structure*

The structure of the treeline ecotone was different in the study sites. (Fig. 2, Fig. 3).

Valtellina (643 individuals sampled) showed the highest species limit (*Pinus cembra*, 2576 m). The uppermost tree > 3 m could be observed at 2400 m (*Larix decidua*); patches of trees >3 m occurred up to 2350 m (transect VT1). The species limit occurred more than 200 m above the tree limit (transect VT1; Table 1). The ecotone showed an overall decline of tree height with increasing altitude to c. 2250 m (Fig. 3), followed by a smoother decrease of tree dimension; the abruptness index for height was always low at the species limit (maximum value 0.20, Table 1). Tree density reached its maximum (1200 individuals ha<sup>-1</sup>; transect VT1) at 2235 m and dropped to 125 individuals ha<sup>-1</sup> at the species limit. *Pinus cembra* was by far the commonest species (86% of the sampled individuals) followed by *Larix decidua* and *Picea abies*.

In Val Camonica (167 individuals sampled) trees were sparser (maximum density 300 individuals ha<sup>-1</sup> at 2360 m); tree species limit (*Larix decidua*) occurred at 2459 m; patches of trees > 3m occurred up to 2340 m (transect VC3), while the isolated uppermost tree could be observed at 2400

m. Tree height declined through a regular gradient (Fig. 3). Abruptness for height at the species limit was slightly higher than in Valtellina (0.24, transect VC2). *Larix decidua* was the dominant species (96% of the sampled individuals), followed by *Picea abies*. In spite of the proximity with the Valtellina site, *Pinus cembra* was completely absent from the study area.

On Mt. Cusna (453 individuals sampled) tree stands were much denser than the alpine ones (up to 2850 individuals ha<sup>-1</sup>); tree and species limit (both *Fagus sylvatica*) were coincident and occurred at 1765 m, where trees up to 8-10 m tall could be found (Fig. 3) The value of abruptness at species limit reached the value of 1.00 both for height and for density (i.e. the maximum height and density was reached at the species limit: transects MC2 and MC4). The commonest species was *Fagus sylvatica* (95.5%) followed by *Sorbus aucuparia*.

#### Age structure

In Valtellina age trend with increasing altitude followed closely that of dimension (Fig 4). Old-growth *Pinus cembra* individuals (up to 500 years old) occurred up to 2300 m; then age decreased sharply and no tree older than 50 years occurred above 2400 m. The uppermost part of the ecotone (above 2500 m) was occupied by *Pinus cembra* seedlings and saplings younger than 5 years, except for a single 45-years old krummholz at 2553 m. Abruptness values for age at the species limit were always very low (maximum value 0.37 at transect VT2).

In Val Camonica, individuals were younger (the oldest specimen was aged 110 years) and age did not follow a clear decreasing trend with altitude (Fig. 4). The colonizing front composed by seedlings and saplings observed in Valtellina could not be found, and the uppermost individuals were from 10 to 50 years old. Abruptness values for age at the species limit were higher than the previous site (0.40 and 0.77 at transects VC1 and VC2, respectively).

At Mt. Cusna, old-growth *Fagus sylvatica* specimens (up to 350 years) occurred at every altitude up to the species limit, together with seedlings and saplings (Fig. 4); the values of abruptness at the species limit were equal to 0.56, 1 and 0.85 at transects MC2, MC3 and MC4, respectively. At transect MC1 forest gaps with strong seedling recruitment could be observed below the treeline; a similar situation was apparent at transect MC2, where few old growth individuals were surrounded by a massive recruitment of seedlings and young saplings in an open forest context. Transect MC3 was characterized by the absence of seedlings and saplings at the uppermost quadrats, where the treeline showed evidence of regression, at least in part due to erosive processes (Fig 5).

#### *PCA of transects attributes*

PCA axis 1 (67.79%) was positively correlated with high abruptness values for density and height and negatively correlated with altitudes of tree- and species limit and their distance. Alpine sites were placed in the field of negative axis 1 coordinates, Apennine sites in the positive one. Axis 2 (16.07%) was positively correlated with abruptness for age and with age of the uppermost individuals; within Alpine sites, Val Camonica occupied the positive field and Valtellina the negative one along this axis (Fig. 6).

#### *PCA of quadrat age structure*

PCA ordination diagram (Fig. 7) showed a gradient from quadrats with marked population increase, with predominant individuals belonging to lowest age classes, to stable and old-growth populations. PCA axis 1 (57.43%) was negatively correlated with seedling and sapling abundance (age class <10 years), while axis 2 (17.79%) was positively correlated with 11-20 and 21-30 years age classes. Plots with prevailing age classes >40 years were positioned in the lower right quadrant of the diagram. At transect level, the analysis confirmed an overall advance trend with old-growth population at lower altitude for Valtellina, a substantially stable trend for Val Camonica throughout

the whole ecotone with few declining populations at lower altitude, and an old-growth stable and locally retreating limit for Mt. Cusna with actively regenerating forest gaps (Fig. 7, lower panel).

#### *Altitudinal limits and temperature data*

Growing season temperature at the tree limit was 5.66°C (5.73° following the criteria defined by Paulsen and Körner 2014) in Valtellina (2350 m), 6.20° (5.95°) C in Valcamonica (2340 m) and 8.45°C (8.65°) at Mt. Cusna. (Table 3). Applying the equation reported by Körner and Paulsen (2004), the corresponding root zone temperatures result equal to 6.03°, 6.30° and 7.42° C, respectively. Coherently, WI was lower in Valtellina (7.91) than in Val Camonica (10.28) and Mt. Cusna (32.00). Continentality was higher in Valtellina following all the indices; Mt Cusna was slightly more continental than Val Camonica according to Gorcynsky's continentality index and  $I_c$ , while slightly less following  $I_{cc}$  (Table 3)

## **Discussion**

#### *Treeline shape and dynamics in the studied sites*

The structure and the dynamic behaviour of the treeline ecotone varied markedly among the study sites, thus confirming our hypothesis 1. Treeline ecotone from Valtellina and Val Camonica could be considered diffuse, as tree height and density decreased gradually from the closed forest to the species limit. Altitudinal limits were generally higher in Valtellina and the distance between tree- and species limit was greater. The main difference between the two Alpine sites could be observed concerning age structure: in Val Camonica the decrease in dimension was not paralleled by a decrease in age, and small but relatively old individuals occurred up to the species limit. For this

reason, that of Val Camonica could be considered a "krummholz" treeline: in fact, 76% of individuals occurring at altitude  $\geq$  the tree limit were multi-stemmed and/or without vertical growth. Only at transect VC2 a dynamic pattern close to those observed in Valtellina could be found (Fig. 7); however, this site is the one affected by past anthropic disturbance, which could have influenced the present dynamics.

Mt. Cusna tree- and forest limit occurred at slightly lower altitudes than those indicated by Pezzi et al. (2008) on the Northern Apennines (1825 m a.s.l.), although most of the treelines mapped by these authors were located below 1725 m. The treeline was clearly abrupt, with sharp passage from forest to open vegetation. Mt. Cusna treeline is strikingly different also for its static trend, with no recruitment few meters above the present tree limit, according with the behaviour of most of the static treelines worldwide as reported by Harsch et al. (2009) and Harsch and Bader (2011).

*Vaccinium* heathlands immediately above the treeline appear very similar to the forest gaps few meters below the treeline abundantly colonized by *Fagus* seedlings (transects MC1 and MC2). Both structural and dynamic features of Mt. Cusna treeline are similar to those observed in some treelines of the southern hemisphere where treeline are mostly abrupt, seedling establishment takes place within 10- 20 m from the tree limit and response to climate warming is often negligible (Cullen et al. 2001; Wardle 2008).

### *Thermal regime*

Thermal regimes differ between Alpine and Apennine sites, in partial contrast with our hypothesis 2. In the Alpine sites, growing season temperature at the tree limit is slightly lower than the value of 6.7°C indicated by Körner and Paulsen (2004) as an average for treelines worldwide and also than the values reported by the same authors for Alpine treelines, which range from 6.3° to 7.7°C; it should be noticed that most of the sites studied by these authors occur at lower altitude than those of

the present study. In both sites, warm month temperatures are close to those indicated by Jobbagy and Jackson (2000) for evergreen conifer treelines (9.3°C at forest line).

Our data confirm the higher temperature of Apennine *Fagus* treeline than those of Alpine sites, even if our values are again lower than those reported by Körner and Paulsen (2004) for central Apennines and are closer to those reported for the temperate zone.

The values of the thermal indices at the local tree limit are slightly higher than the extreme limits reported by Fang and Lechowicz (2006) for the upper distribution limits of *Fagus sylvatica*: WI index is equal to 32°C month (vs. 28°C month at the extreme limit following these Authors); ABT is = 5.5°C (vs. 5.2°C); average temperature is =4.99° C (vs. 4.5°C) (Table 3). Warm month temperatures are higher than those reported by Jobbagy and Jackson (2000) for broadleaf deciduous treeline (8.5°C). Our data agree with global data indicating that abrupt treelines generally occur at lower elevations than those expected in agreement with growing season temperature and are often formed by broadleaf species (Harsch & Bader 2011). Again, this pattern is close to those observed at southern hemisphere *Nothofagus* treelines (Wardle 2008).

The comparison between our temperature value and those reported by Körner and Paulsen (2004) should take into account the different origin of data: directly measured *in situ* for 1-3 years for the cited Authors and obtained from interpolation of decadal data of official weather stations in the present work. However, the general pattern of our data is coherent with the global one provided by those Authors.

#### *Comparison between different treeline types*

Our fine-scale study confirmed the pattern outlined by global scale analyses concerning the relationships between climatic features, treeline shape, dominant species phenology and present dynamics.



Within conifer treelines many important differences could be observed, particularly striking as our alpine study areas are less than 10 km apart. Diffuse treelines (Valtellina) confirmed their equilibrium with growing season temperature and their sensitivity to present warming (Harsch & Bader 2011) resulting in active advance. These treelines reach the uppermost altitudes, and seedling recruitment is effective well above the present tree- and forest limit.

Our krummholz treelines (Val Camonica) could be considered "diffuse" from the dimension and density point of view and "abrupt" from that of age structure. The species limit is lower than that of Valtellina mainly because of the lack of colonizing front of seedlings. Krummholz treelines are supposed to be mainly limited by dieback (Harsch & Bader 2011). In our case, a lack of recruitment seems to be important, which can be due to high seedling mortality, low germination rates or to a less effective dispersal strategy of *Larix decidua* compared with zoochorous *Pinus cembra* (Holtmeier & Broll 2007; Lingua et al. 2008). Species composition seems to be determining for treeline behaviour, and is probably linked to climatic continentality, *Pinus cembra* being less adapted to relatively oceanic climates (Theurillat & Schlüssel 2000; Caccianiga et al. 2008). The overall low density of the population may also play a role.

In Valtellina, podzolic soils occur at high altitude (Angelucci et al. 1993) up to c. 2600 m (C. Compostella, L. Trombino, M. Caccianiga, unpublished), suggesting that long term dynamics of tree and forest limit was characterized by important altitudinal variations during the Holocene; no data are available about species composition of those past elevated treelines. In Val Camonica, abundant subfossil *Pinus cembra* logs, up to 7 m tall, found at c. 2400 m at the site of transect VC3 and dated to early-mid Holocene (Ravazzi & Aceti 2004; C. Compostella, unpublished) indicated a past high position of the tree- and probably forest limit, but linked to different species composition (*Pinus* instead of *Larix*).

Concerning the Apennine abrupt treeline, our data suggest that the present upper limit of *Fagus* are close to the thermal threshold for the species, as suggested by Körner and Paulsen (2004). In this

case, the present treeline position could be the contingent result of the historical events which led to the present species composition, while different species could have resulted in higher treeline; the possibility for conifers to occupy higher positions than present broadleaved oceanic treelines has been documented in the southern hemisphere after the introduction of alien conifer species (Wardle, 1985, 2008). In the Northern Apennines the role of species composition could be supported by archaeological and paleoecological records (Cremaschi et al. 1984; Compostella et al. 2012) indicating a past occurrence of forest vegetation at least up to 2000 m on Mt. Cusna during the early-mid Holocene, but with no evidence of *Fagus*. A prominent role of *Abies alba* in the Apennines throughout the Holocene is likely, as suggested by Watson (1996), Vescovi et al. (2010a,b), Körner (2012) and Compostella et al. (2012); its replacement by *Fagus* was probably at least in part induced by human activity (Carcaillet & Muller, 2005; Vescovi et al. 2010a,b); the marginal role of *Picea abies* could be the result of ineffective spread due to unfavourable climatic conditions and competition during the Holocene (Ravazzi et al. 2006).

The lack of response of the Apennine treeline could be due to other climatic parameters than temperature alone limiting seedling recruitment or enhancing seedling mortality above the present limit (Kollas et al. 2012). Spring frost is known among the limiting factors for the upwards growth of *Fagus*, particularly for seedlings (Bernetti 1994). With climate warming, upward shift of beech could be limited by the increase in late frost damage due to anticipated bud opening (Cailleret & Hendrik 2010). Winter temperatures could represent a limiting factor for hardwood species (Wardle 2008) while summer temperatures, described as determining factors also for oceanic treelines by Jobbagy and Jackson (2000) do not seem to be limiting. In any case, *Fagus* at the Apennine treeline does not show the advancement of recruits above the adult tree limit observed by Vitasse et al (2012) in the Swiss Alps.

The present research made it possible to perform a comparison between completely different treeline types in a relatively small area through a standardized, detailed sampling, **and provided**

**useful information for predicting treeline dynamics at widescale.** Our results highlighted the role of species composition in determining shape and dynamics of the treeline ecotone; species composition is, in turn, determined by climatic features and historical (including man-driven) events. Our analyses emphasized the necessity of combination of researches at different scales, to take into account both the general rules underpinning treeline position and the complex interaction of environmental factors at site and microsite level. **The responses of treelines at global scale to climate warming are not straightforward and may vary from fast reaction to almost unresponsive situations, the latter occurring in many sites throughout the world but still poorly explored and understood (Harsch et al. 2012). An integration with historical and paleoecological data can provide further information for the understanding of the factor globally driving treeline position; putting local data in a wider frame may allow a better comprehension of the mechanisms and the contingent events which determined the present situation and the ongoing dynamics.**

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## Figure captions

**Fig.1** Study areas. Stars: transects; squares: weather stations; triangles: major peaks. Grey lines: mountain ridges; thin black lines: rivers; thick black line: country boundary. Grey areas indicate National Parks

**Fig. 2** Views of the treeline in the three study areas. Pictures were taken close to the species limit. From top to bottom: sparse seedlings and saplings of *Pinus cembra* at the Valtellina site (transect VT1); sparse and stunted individual of *Larix decidua* at Val Camonica (transect VC2); abrupt tree- and species limit formed by *Fagus sylvatica* at Mt. Cusna (transect MC4)

**Fig. 3** Tree height/altitude relationship for each transect in the three study areas. Each point represents a single individual. Overlapping points are not shown.

**Fig. 4** Tree age/altitude relationship for each transect in the three study areas. Each point represents a single individual. Overlapping points are not shown

**Fig. 5** Treeline at transect MC3 (Mt. Cusna Area)

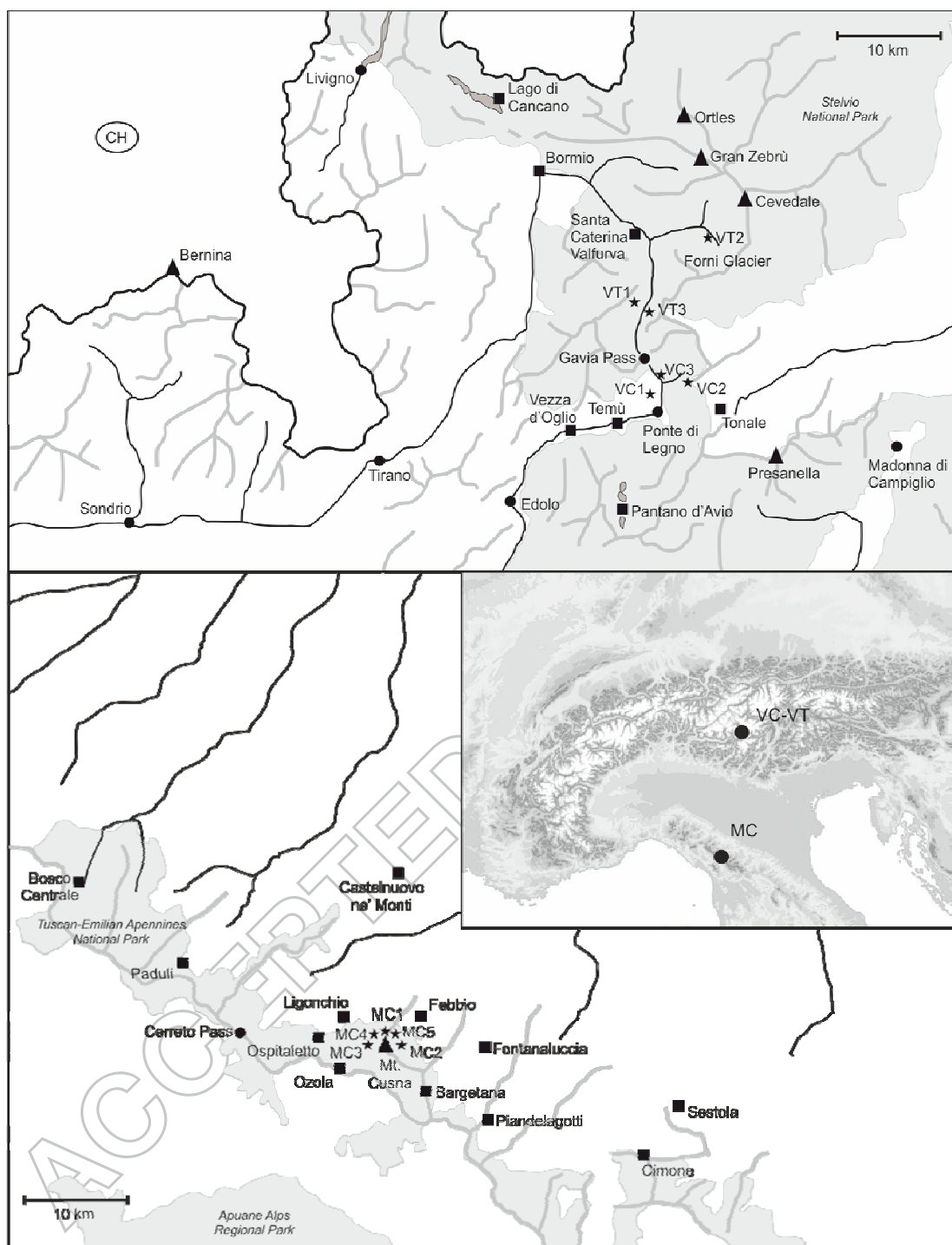
**Fig. 6** PCA biplot based on selected transect attributes (see text). PCA axis 1 (67.79% of variance) and axis 2 (16.07%) are displayed;

Dist Tree-Species limit: distance (i.e. altitudinal difference) between tree- and species limit;  
Density: maximum density; Abr Age Sp limit: Abruptness value for age at the species limit; Abr Height Sp limit: Abruptness value for height at the species limit; Abr Density Sp limit: Abruptness value for density at the species limit; Age 90th: mean age of the individuals recorded the altitudinal 90th percentile

**Fig. 7 a):** PCA ordination diagram of quadrats based on age class distribution of individuals. PCA axis 1 (57.43% of variance) and axis 2 (17.79%) are displayed. Triangles indicate quadrats from Valtellina, circles those from Val Camonica, and squares those from Mt. Cusna. Black symbols indicate the uppermost quadrat of each transect.

b): position of each quadrat within the transects. Grey scales indicate the dynamic behaviour as inferred from PCA (see text). Quadrats with less than 5 individual were not included in the analysis and are written in italic.

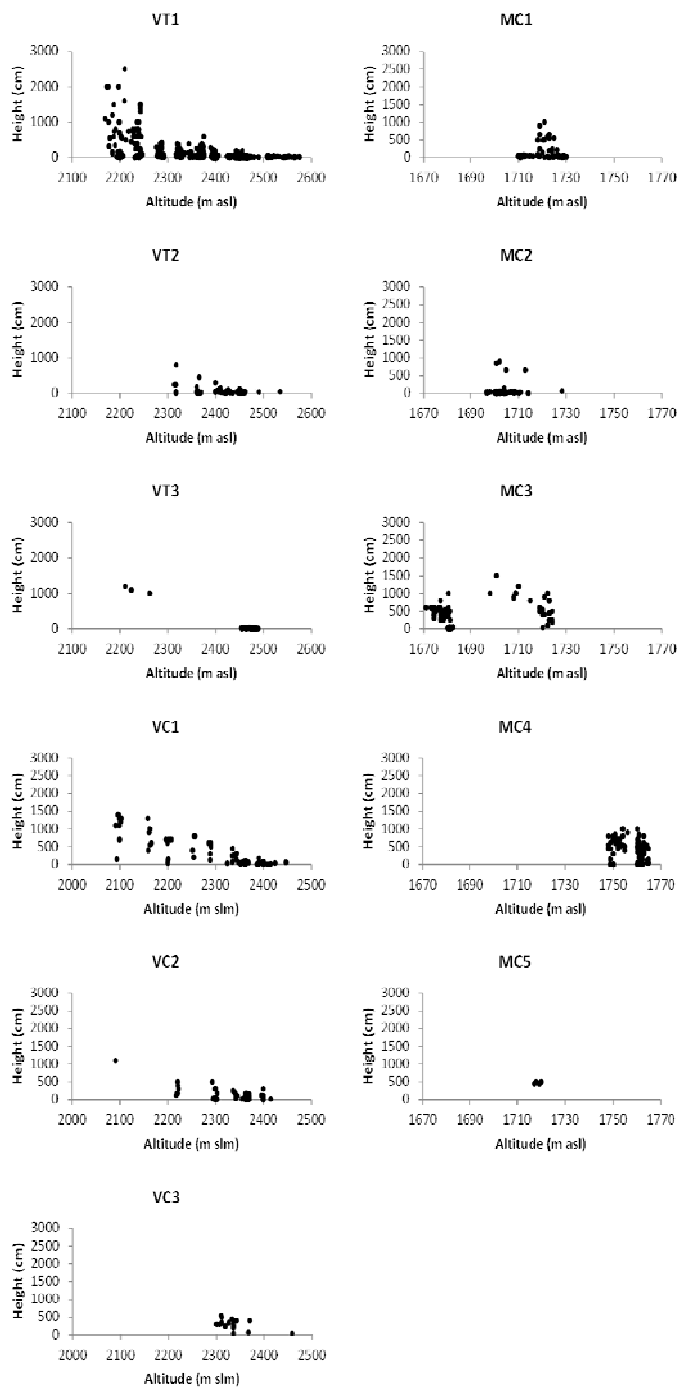
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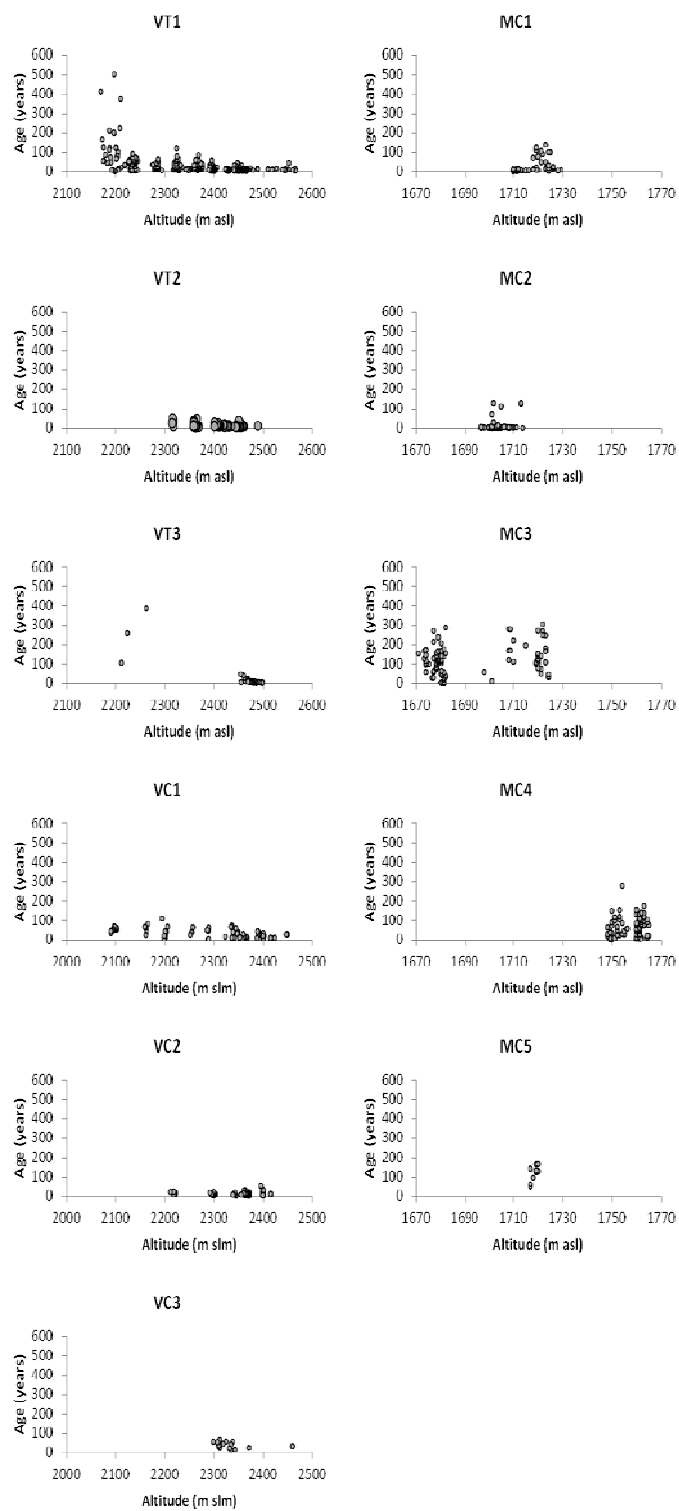


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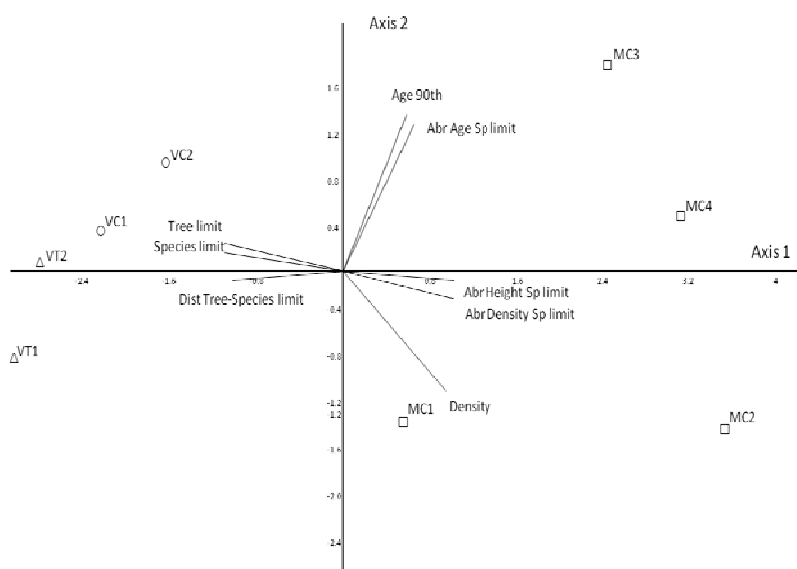


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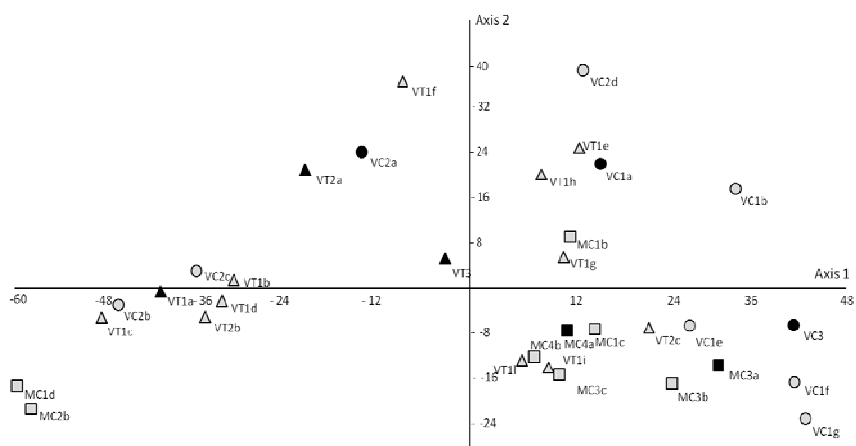


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VT1a	VT2a	VT3	VC1a	VC2a	VC3	MC1a	MC2a	MC3a	MC4a	<table border="1"> <tbody> <tr> <td>Expanding</td> </tr> <tr> <td>Stable</td> </tr> <tr> <td>Oldgrowth</td> </tr> </tbody> </table>	Expanding	Stable	Oldgrowth
Expanding													
Stable													
Oldgrowth													
VT1b	VT2b		VC1b	VC2b		MC1b	MC2b	MC3b	MC4b				
VT1c	VT2c		VC1c	VC2c		MC1c		MC3c					
VT1d			VC1d	VC2d		MC1d							
VT1e			VC1e										
VT1f			VC1f										
VT1g			VC1g										
VT1h													
VT1i													
VT1j													
VT1	VT2	VT3	VC1	VC2	VC3	MC1	MC2	MC3	MC4				

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Table 1. Transect data. Abruptness data are not given for transects consisting of a single quadrat.

\*Tree limit altitude for transect VT3 was assessed only by aerial imagery, as the quadrat of transect VT3 was placed above the tree limit.

Area	Transect	N of trees	N of quadrats	Tree limit (m a.s.l.)	Species limit (m a.s.l.)	Distance tree-species limit	Max density (individuals/ha)	Abruptness age at species limit	Abruptness height at the species limit	Abruptness density at the species limit	Mean age 90th percentile
Valtellina	VT1	510	10	2350	2576	226	1200	0.08	0.04	0.1	10.4
Valtellina	VT2	89	3	2320	2534	214	475	0.37	0.2	0.05	8.2
Valtellina	VT3	41	1	2320*	2499	179	-	-	-	-	-
Val Camonica	VC1	67	7	2320	2450	130	300	0.4	0.05	0.25	19.9
Val Camonica	VC2	80	4	2300	2415	115	200	0.77	0.24	0.214	13
Val Camonica	VC3	20	1	2340	2459	119	-	-	-	-	-
Mt. Cusna	MC1	115	4	1725	1730	5	1775	0.16	0.1	0.26	8
Mt. Cusna	MC2	116	2	1713	1714	1	2850	0.56	1	0.98	20.7
Mt. Cusna	MC3	111	3	1724	1724	0	1325	0.85	0.48	0.38	148
Mt. Cusna	MC4	100	3	1765	1765	0	1775	1	0.68	1	54.8
Mt. Cusna	MC5	9	1	1720	1720	0	-	-	-	-	-

Table 2. Weather stations used for the calculation of the thermal altitudinal gradient. Stations used for the calculation of climatic features and indices at the treeline are in bold. Source: Environmental Regional Agencies (ARPA) of Emilia-Romagna and Lombardy regions, of Trento province (Meteotrentino) and Istituto Idrografico del Po, Annali Idrologici.

<b>Study site</b>	<b>Station</b>	<b>Latitude</b>	<b>Longitude</b>	<b>Altitude</b>	<b>Observation period</b>
Valtellina	<b>Santa Caterina Valfurva</b>	<b>46°25'</b>	<b>10°30'</b>	<b>1740</b>	<b>1973-2009</b>
Valtellina	Bormio	46°28'	10°22'	1225	1955-1984
Valtellina	Lago di Cancano	46°32'	10°19'	1948	1978-1998
Val Camonica	<b>Tonale</b>	<b>46°15'</b>	<b>10°34'</b>	<b>1875</b>	<b>1973-2009</b>
Val Camonica	Temù	46°15'	10°28'	1100	1955-1984
Val Camonica	Veza d'Oglio	46°14'	10°24'	1070	1955-1984
Val Camonica	Pantano d'Avio	46°10'	10°28'	2325	1955-1984
Mt. Cusna	<b>Ligonchio</b>	<b>44°31'</b>	<b>10°35'</b>	<b>928</b>	<b>1973-2009</b>
Mt. Cusna	Ospitaletto	44°29'	10°31'	1140	1961-1990
Mt. Cusna	Cimone	44°21'	10°70'	2165	1961-1990
Mt. Cusna	Piandelagotti	44°21'	10°53'	1209	1961-1990
Mt. Cusna	Paduli	44°35'	10°13'	1139	1961-1990
Mt. Cusna	Sestola	44°23'	10°76'	1020	1961-1990
Mt. Cusna	Bosco centrale	44°43'	10°03'	748	1961-1990
Mt. Cusna	Ozola	44°28'	10°36'	1220	1961-1990

Table 3. Monthly temperatures and values of the climatic indices calculated at the treeline in the 3 study areas;  $r^2$  values for the linear regression are given for each month. Ic= continentality index; GS= Growing season temperature; Icc= continentality index compensated for altitude; WI= Kira's warmth index; ABT= Holdridge's annual biotemperature; CI= Kira's coldness index; K= Gorcynsky's continentality index.

Site	Altitude	J	F	M	A	M	J	J	A	S	O	N	D	Year	Ic	GS	Icc	WI	ABT	CI	K	
Valtellina	2350	-	-	-	-	1.	6.	8.	8.	4.	-	-	-	-	19	5.	33	7.	2.	-	25	
		.11	.11	6.	3.	80	14	49	28	22	0.	6.	9.	1.	.6	6	.7	91	4	89	.9	
		.13	.78	58	71						65	35	84	7	2	6	2		1	.0	7	
$r^2$		0.	0.	0.	0.	1.	0.	0.	1.	0.	0.	0.	0.									
		.71	.82	.97	.99	.00	.99	.99	.00	.98	.85	.72	.56									
		.73	.31	.40	.07	.08	.03	.08	.01	.03	.08	.01	.08									
Val Camonica	2340	-	-	-	-	3.	6.	8.	8.	6.	1.	-	-	0.	15	6.	29	10	2.	-	16	
		6.	7.	4.	1.	00	97	78	36	17	99	1.	5.	6	.4	2	.4	.2	9	62	.0	
		62	06	36	66							37	99	8	0	0	4	8	4	.0	0	
$r^2$		0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.									
		.53	.77	.88	.84	.84	.92	.83	.83	.85	.67	.79	.53									
		.11	.11	.09	.00	.02	.04	.05	.09	.00	.08	.06	.04									
Mt. Cusna	1760	-	-	-	2.	6.	11	14	13	10	6.	1.	-	4.	16	8.	26	32	5.	-	17	
		2.	2.	0.	20	94	.0	.0	.3	.4	21	81	0.	9	.1	4	.7	.0	5	32	.7	
		11	85	33			2	4	5	5			80	9	5	5	1	0	0	.0	7	
$r^2$		0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.	0.									
		.92	.92	.93	.94	.93	.91	.92	.92	.92	.88	.92	.90									
		.44	.45	.47	.44	.46	.47	.43	.44	.42	.46	.44	.44									