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Snow Fungi–Induced Mortality of *Pinus cembra* at the Alpine Treeline: Evidence from Plantations

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Abstract

Identifying the factors controlling tree mortality is key to understanding the effects of ongoing global change on treeline movement and species composition. One potentially significant but little studied factor that impacts the formation of treelines is mortality caused by snow fungi. We studied the mortality patterns of *Pinus cembra*, a typical treeline species of the Central Alps of Switzerland, in two plantations located on opposite slopes of the Dischma valley (Northeast [NE] and Southwest [SW]) above the current treeline. In 1975, 33,000 *P. cembra* trees were planted at the NE site and 550 trees at the smaller SW site. All trees have been periodically monitored for survival since then. After 30 years, only ca. 5% of all *P. cembra* trees survived in both plantations. Two species of pathogenic snow fungus, *Gremmeniella abietina* and *Phacidium infestans*, were major mortality agents for saplings. High rates of infection by *Gremmeniella* corresponded to late snowmelt and high ratios of rainfall to temperature. High rates of infection by *Phacidium* corresponded to earlier snowmelt and were spatially associated with *P. cembra* mature trees that had been present in the area before the time of planting. We provide experimental evidence that snow fungi are a primary cause of sapling tree mortality at treeline. Although additional evidence from different geographic regions and more natural treeline distributions is needed, our results suggest that the prevalence of snow fungi may prevent establishment of trees above the current treeline at present, and under future climate scenarios.

Introduction

High-elevation treelines, the lines connecting the uppermost adult tree patches within a given slope (sensu Körner, 1998), are one of the most distinct vegetation boundaries worldwide, and are considered particularly responsive to climate change (e.g., Tranquillini, 1979; Germino et al., 2002; Wieser and Tausz, 2007). As climate has been warming, treelines have moved upwards in various mountain regions in the world (Luckman and Kavanagh, 2000, in the Canadian Rocky Mountains; Kullman, 2002, in the Scandes; Camarero and Gutiérrez, 2004, in the Pyrenees; Shiyatov et al., 2007, in the Ural Mountains; Vittoz et al., 2008, in the Alps). Other studies, however, do not report a rise in alpine treeline; one even reports stable behavior for thousands of years (Ives and Hansen-Bristow, 1983). Harsch et al. (2009) observed that approximately 50% of treelines around the world have recently advanced. For certain treelines, the apparent stability can be explained by a lagged response to higher temperatures or land use change at or above the current treeline (e.g., Hofgaard, 1997, in the Scandes Mountains; Camarero and Gutiérrez, 2007, in the Pyrenees; or Gehrig-Fasel et al., 2007, and Wallentin et al., 2008, in the European Alps). Moreover, seedling establishment at treeline has been related to topographical variation. An advance of treeline on south-facing slopes and no advance on north-facing slopes have been related to the differential presence of permafrost (Danby and Hik, 2007) or to soil moisture availability (Daniels and Veblen, 2004). However, no differences between north- and south-facing slopes were observed in the Swiss Alps (Paulsen and Körner, 2001). Furthermore, closed vegetation cover of herbaceous plants or shrubs may prevent the seeds of common wind-dispersed treeline species in the Alps

such as European larch (*Larix decidua* L.) from reaching a suitable seedbed (Risch et al., 2003). Swiss stone pine (*Pinus cembra* L.), however, a typical climax species of alpine treeline ecosystems, is mainly dispersed by a bird, the Eurasian nutcracker (*Nucifraga caryocatactes*), that buries the seeds in caches, as winter food, and places them into favorable microsites for germination and establishment. Therefore, the Swiss stone pine has the potential to colonize higher elevations even with shrub encroachment (Didier, 2001, in the French Alps; Lingua et al., 2008, in the Italian Alps). There is hence evidence that trees at the treeline might migrate upwards, but the elevation, shape, and species composition of a future treeline remains largely uncertain. We must understand all factors driving treeline formation in order to predict future changes in these ecosystems.

Although temperature is considered to govern treeline position at large scales (Körner, 2003; Körner and Paulsen, 2004), other environmental factors strongly influence tree mortality and growth patterns at multiple spatial scales (reviewed by Holtmeier and Broll, 2005). At certain treelines, ample snow cover during the winter promotes seedling establishment and growth by enhancing soil moisture and nutrient uptake or protecting the small trees from wind abrasion (Sveinbjörnsson et al., 2002, tundra-taiga interface; Hughes et al., 2009, Caucasus Mountains; Batllori et al., 2009, Pyrenees). However, deep snow promotes the growth of certain fungi. Seedling survival at alpine treeline ecosystems has been linked to subtle changes in the duration of snow cover in spring, with clear thresholds of increasing mortality related to a late snowmelt date (Barbeito et al., 2012). Therefore, in regions with heavy snowfall, the negative impacts of the fungal diseases associated with snowpack can outweigh the protective role of snow and cause

mortality among seedlings and young conifers (i.e., while they remain below the average winter snow cover) at treeline (Hättenschwiler and Körner, 1995, and Senn, 1999, in the Alps; Kullman, 2007, in the Scandes). Nevertheless, snow fungi influence on the treeline has rarely been quantified or been analyzed systematically.

One of the few well documented examples for potential disruption of the treeline establishment resulting from pathogen dynamics is the case of whitebark pine (*Pinus albicaulis*) in the Rocky Mountains, infected by the invasive fungal pathogen *Cronartium ribicola*, which causes white pine blister rust (Tomback and Resler, 2007; Resler and Tomback, 2008). Mortality by blister rust reduces the seeds available for the nutcracker to disperse to the alpine treeline and ends the facilitative role of whitebark pine in tree island initiation, altering the community structure (Resler and Tomback, 2008). Swiss stone pine, like whitebark pine, is a five-needle pine. Seedlings and saplings of this species are commonly killed by snow fungi within a few years of initial infection (Senn, 1999), mainly by *Gremmeniella abietina* (Lagerb) Morelet and *Phacidium infestans* P. Karst. Both parasitic fungi are common pathogens in the circumpolar boreal forest zone, characterized by mycelial growth under the snowpack (Ranta and Saloniemi, 2005). *Gremmeniella* is a pathogen with a wide distribution and extensive host range (dozens of conifer species, especially of the genus *Pinus*; Ranta and Neuvonen, 1994), while *Phacidium*, although widely distributed in mountainous regions of the northern hemisphere, occurs only on *P. cembra* in the Alps. While *Gremmeniella* attacks mainly weakened trees, *Phacidium* attacks trees regardless of their condition (Holtmeier, 2009). While *Gremmeniella* spreads mainly by wind and summer splash water (Votila, 1985), *Phacidium* infection transmission occurs also by direct needle contact and thus a great majority of infections occur close to the source (Nierhaus-Wunderwald, 1996). Attack by *Gremmeniella* and *Phacidium* is focused on trees up to 50 years old, which is the time that trees may take to grow above a 1.5-m-deep snow cover at treeline (Holtmeier, 2009).

Major snow fungi outbreaks have been attributed to high precipitation and low average temperature during the host's growing season, which favor pathogen sporulation and dispersal (e.g., La Porta et al., 2008; Thomsen, 2009). The duration of snow cover affects fungal growth both in terms of water availability and the insulating properties of snow (Schmidt et al., 2012). A thicker snow cover and late snowmelt have been related to massive needle death in spruce trees by snow fungi and subsequent tree mortality (Auger and Payette, 2010). Empirical data from the period 1930–2010 suggest that climate change may be already reducing snow depth and moving up the date of snow disappearance in spring above 1500 m (Marty and Meister, 2012). At the Swiss Alps treeline, a significant increase in temperature and subsequent earlier snowmelt have been reported for the period 1975–2010 at 2090 m (Rixen et al., 2012). The role of plant-pathogen interactions in modulating ecosystem response to climate change is still poorly understood (e.g., Wiedermann et al., 2007), although it undoubtedly affects the main ecological processes structuring treeline ecotones (Harsch et al., 2009).

Two major reasons for the difficulty in drawing conclusions about treeline long-term responses to pathogens are the scarcity of long-term data sets and the lack of controlled field studies (Speed

et al., 2010; Barbeito et al., 2012). Observational studies provide relevant spatial information on variation of snow fungi infection rates among sites (e.g., Smith et al., 2011) but only provide a snapshot in time and cannot give information about the spread of the fungi. To achieve a complete and accurate assessment of fungi spread, two high-elevation plantation experiments were monitored to assess fungi infection patterns for 30 years, across tree establishment, in addition to a spatial analysis of site differences. Our study may be the first to explore the effect of snow fungi on alpine treeline mortality across a broad spatial scale over multiple years. The two plantations were located on northeast (NE) and southwest (SW) exposed slopes at or slightly above the natural climatic treeline in the Swiss Alps. We investigated the infection and spread of *Gremmeniella* and *Phacidium* and their impact on the mortality patterns of *P. cembra*. We hypothesized that mortality by snow fungi should be higher on the NE aspect where snowmelt is delayed compared to the SW aspect. We further used the much larger plantation on the NE slope to ask: (1) Which factors had the greatest influence on *Gremmeniella* and on *Phacidium* spatial patterns of infection over time? We hypothesized that snowmelt date would be the main factor shaping the infection pattern. And (2) Can we attribute the episodes of snow fungi mortality at treeline to extreme snow conditions? We hypothesized that years with long snow cover in spring would be followed by higher fungi infection rates.

Material and Methods

RESEARCH SITES

Our study was conducted at two plantation research sites located on the opposite slopes of the Dischma Valley in the central Alps (Switzerland), in NE and SW exposures (Appendix Fig. A1). In 1975, ca. 92,000 (NE) and 1650 (SW) seedlings of three high-elevation conifer species (*Pinus cembra* L., *Pinus mugo* ssp. *uncinata* Ramond, and *Larix decidua* L.), each two to five years old, were systematically planted in 4052 and 66 square plots in the NE and SW plantations, respectively (ca. 1350 and 22 plots for each species). Plots in both experiments were 3.5 m by 3.5 m arranged in a quadratic grid, with 25 trees in each plot planted into the original dwarf shrub community at 70-cm intervals. The large NE plantation covers 5 ha of a topographically complex slope (9.4 to 59.7%) starting at the current treeline (at ca. 2100 m a.s.l.; Barbeito et al., 2012) and covering an altitudinal gradient of more than 150 m (2080 to 2230 m a.s.l.). The SW plantation is much smaller (0.8 ha) and covers an altitudinal gradient of only 20 m with a very uniform slope (30 to 35%). The elevation range of the SW plantation corresponds to the mid-elevation section of the NE site (2175 to 2195 m a.s.l.). In addition to the *P. cembra* trees planted in 1975 (ca. 33,000 trees at the NE site and 550 at the SE site), 82 *P. cembra* mature trees (Fig. 1) with an average age of 100 years (P. Bebi, unpublished data) were present at the NE site at the time of planting. All of these mature trees are infected by *Phacidium* in the lower branches (i.e., the ones below the snow cover). At the SW site there are no mature *P. cembra* trees within the plantation, but there are groups of them 50 m away. Climate data since 1975 are available from a meteorological station located near the bottom of the NE site (2090 m a.s.l.). The annual air temperature averaged 2.0 °C, and the annual precipitation was 1150 mm (1975 to 2005 mean). The average winter snow cover at the meteorological station

1975
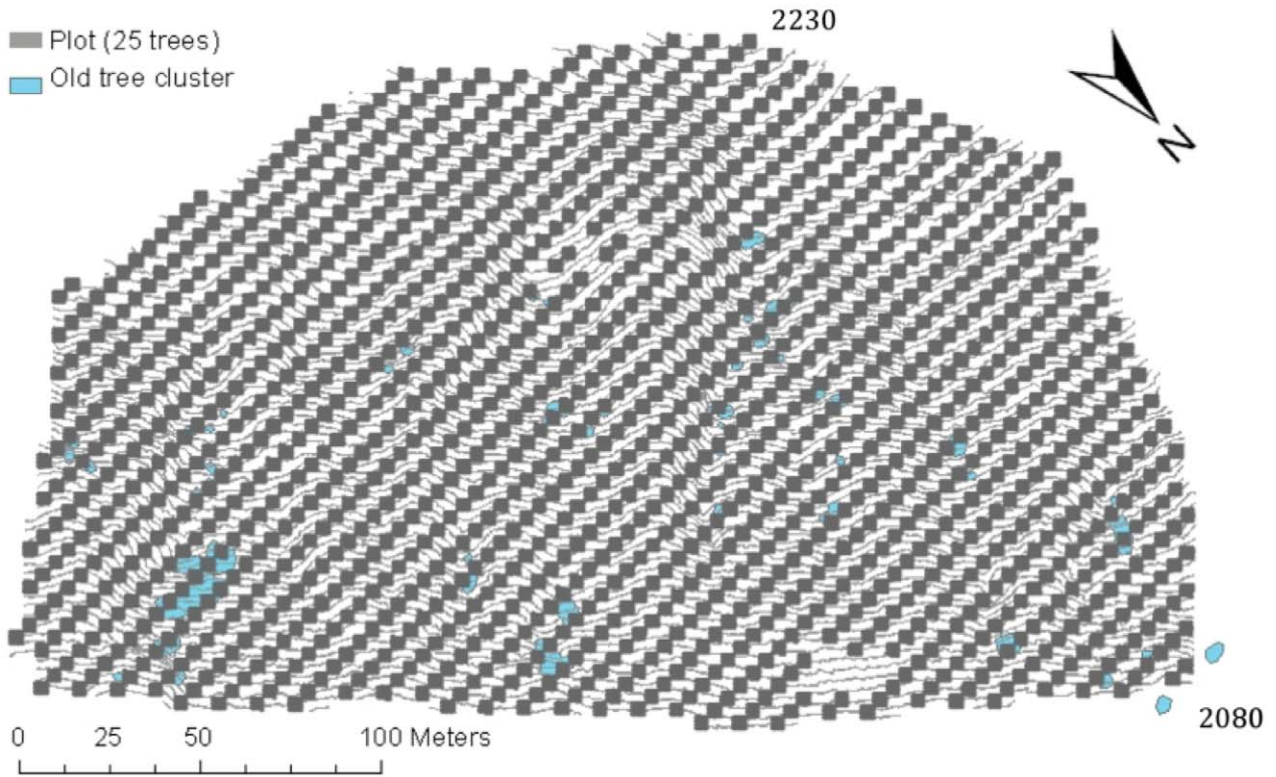
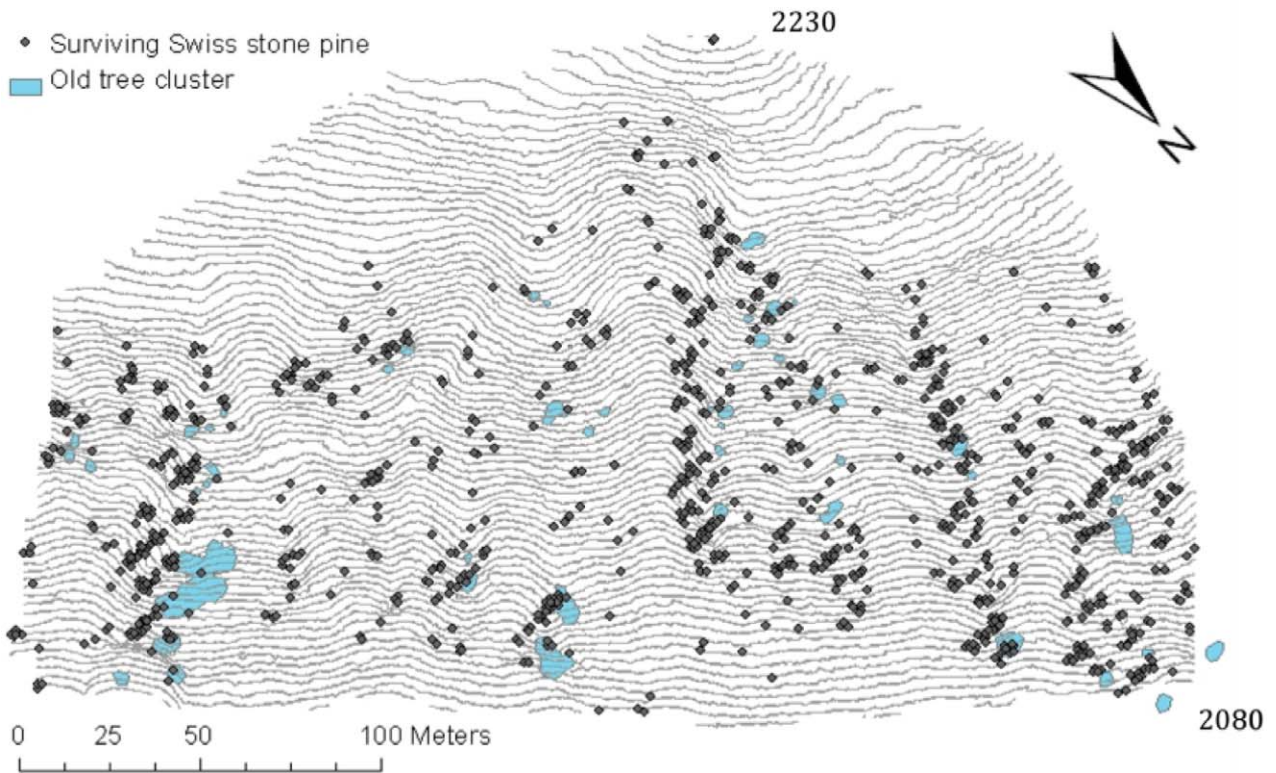
FIGURE 1. *P. cembra* **planted trees and mature pine tree clusters distribution map of the NE plantation experiment, Central Alps, Switzerland, in 1975 (squares represent plots; with 25 trees per plot) and in 2010 (dots represent trees).**

lasts from mid-October to the end of May, with an annual maximum snow depth of 1.46 m (1975–2005 mean). The study site was fenced to avoid animal browsing, and only slight damage from chamois (*Rupicapra rupicapra* L.) and black grouse (*Tetrao tetrix* L.) browsing occurred, which affected height growth of several trees but did not kill any during the observation period (Senn, 1999). The temporal development of fungal infection and subsequent mortality were analyzed for all the planted trees of the SW site and for all trees in a subsample area of the NE site with the same size and number of trees as the SW site, and with a similar elevation and slope. Mortality was recorded annually from 1975 to 1995 in all the trees from both plantations and once more in 2005. Yearly data on fungal infection (presence/absence) and mortality cause were recorded during the first 20 years after planting (1975 to 1995) for all trees in the SW site and the NE subsample.

SNOW FUNGI SPECIES

The fungal diseases were identified visually on all *P. cembra* trees according to the typical infection symptoms (identified by Roll-Hansen, 1989). Infections by *Gremmeniella* cause a loss of needles on the youngest shoots, with the remaining needles turning red (Appendix Fig. A2) and starting to die at the base. Infection by *Phacidium* causes needles to die below the snowpack (i.e., lower part of the tree), leading to brownish needles in the following summer and bleaching to nearly white the year after (Appendix Fig. A2). The losses of *L. decidua* by *Gremmeniella* were only ca. 1% and thus we excluded this species from the study. In contrast, *Gremmeniella* was identified as the killing agent of almost 70% of dead *P. mugo* until 1995 (Senn, 1999). The prostrate form of *P. mugo* was planted because of its potential for high altitude afforestation and as protection against avalanches and erosion in many parts of the Alps, and because it performed in preliminary afforestation experiments on the same slope much better than other species such as *P. abies* (Schönenberger, 1975). *P. mugo* occurs naturally in the central Alps, but not on the slopes of the two plantations. Because there will be little impact on the response of natural treeline to climate warming from infection of *P. mugo*, we excluded it from the study. Moreover, since *P. cembra* is the predominant tree species of the treeline in the study area, we focused on fungi infection of this species, and only considered *P. mugo* infected trees by *Gremmeniella* as a possible source of the fungus spread. We found no significant spatial association between the infected trees of both pine species (results not shown).

STATISTICAL ANALYSES

To analyze the spatial development of fungal infection over time and its relationship with the environmental factors recorded at the plot scale, we only used data from the largest NE plantation site. A full survey of the fungal infection was available for 1979, 1982, 1985, and 2010. For each plot of 25 trees within the NE site, many micro-site characteristics were recorded at the time of planting, but we selected only relevant and non-collinear variables (see Barbeito et al., 2012): elevation (2080 to 2230 m a.s.l.), topography based on exposure and slope (four microsites: North, East, Gully, Ridge), wind velocity (0.95 to 3.42 m s^{-1}, measured in 1971, four years before planting), and initial date of snowmelt in

spring (recorded for each square plot of 25 trees and averaged between 1975 and 1982; day 123, 3 May, to day 170, 19 June, where day 1 is 1 January). Wind speed, an environmental factor that can potentially influence the pattern of fungal spore transport, was measured at 1 m height with 60 anemometers distributed in a 20×20 m grid covering the whole plantation. The spatial pattern of initial snowmelt date was only recorded at the time of tree establishment and was more influenced by topography than by precipitation and temperature (Barbeito et al., 2012). There was no change in snow distribution spatial patterns across the NE site over the period 1975–2005 (verified with orthophotos of the study site at the time of planting and 30 years later; Barbeito et al., 2012), so although this variable was only recorded at the beginning of the study, it was relevant for the entire study period. We used decision-tree based analysis (DT; Breiman et al., 1984) to determine relationships between the fungal infection by *Gremmeniella* and by *Phacidium* at the NE site and the set of explanatory variables. DTs are models that build rules for assigning observations into classes using numerical and/or categorical predictor variables. These rules are built by recursive binary partitioning on a set of categorical or numerical variables into regions that are increasingly homogeneous with respect to the response variable, with the results displayed on a dendrogram (De'ath and Fabricius, 2000). We used an unbiased classification tree algorithm that employs *P*-values for variable selection and as a stopping criterion (Hothorn et al., 2006). We chose a conservative *P*-value ($P < 0.001$) for our study because of the large sample size. DTs were carried out in R 2.12.2 for Windows (R Development Core Team, 2010), using the ''party'' package (Hothorn et al., 2006).

All mature *P. cembra* trees were mapped at the NE plantation, and for each tree two perpendicular crown diameters were recorded. Given that most of these trees were located in the lower part of the plantation and on the ridges, a neighborhood variable such as distance to the closest mature *P. cembra* tree would be highly collinear with the other selected variables (i.e. elevation and topography), and therefore we decided to analyze this effect separately. Spatial point pattern analysis has been commonly used to quantify and model the spatial patterns of forest diseases (e.g. Liu et al., 2007) and to detect processes operating at the upper treeline (Elliott and Kipfmueller, 2010). To assess the potential influence of the mature *P. cembra* trees present at the time of planting on the spread of snow fungus infection, we used the bivariate extension of the pair-correlation function $g_{12}(r)$ that can identify patterns at varying spatial scales (Stoyan and Stoyan, 1994). We used a grid-based approach to model surfaces rather than points, incorporating canopies (Barbeito et al., 2008). To investigate if plants of one pattern are not randomly distributed within the neighborhood of the plants of another pattern, the appropriate bivariate null model keeps pattern 1 fixed (mature tree crowns) and randomly distributes the plants of pattern 2 (planted trees) over the parts of the study area not occupied by pattern 1 (called antecedent condition; Wiegand and Moloney, 2004). We tested the measured pattern against the 5 lowest and 95 highest simulated values of the antecedent condition null model for each distance generated using 999 Monte Carlo simulations. Values of $g_{12}(r)$ greater or less than 1 indicate attraction or repulsion between the two patterns, respectively. Point pattern spatial analyses were performed using the software Programita (Wiegand and Moloney, 2004).

The yearly data on mortality and infection were used to calculate the infection time before death for each fungi species at both plantations. Death of trees is likely triggered by the fungi attack but it may also be caused by other mortality agents in combination with the fungi (Franklin et al., 1987). We examined the association of snowmelt date and maximum snow depth (measured at the meteorological station at the NE site) with the following year's infection by *Gremmeniella* and *Phacidium* for the period 1975–1995. We calculated the *Gremmeniella* index value (GIV; Thomsen, 2009), an index that has shown a positive correlation with the fungus outbreaks (Thomsen, 2009), and is defined as the total rainfall of the month divided by the average temperature. We calculated the GIV for each month of the average growing season at our site (June to September). We analyzed the relationship between the conditions of the previous growing season's GIV and the following years' infection by *Gremmeniella* for the 20 years of climate data and annual infection data.

Results

Thirty years after planting, ca. 5% of *P. cembra* trees had survived in both plantations at the NE and SW sites (Fig. 2), with the highest mortality occurring between 10 and 15 years after planting. The percentage of surviving trees and yearly *P. cembra* mortality in the subsample chosen on the NE site was very similar to that observed for the whole NE plantation (Barbeito et al., 2012). For the first 20 years, when most of the mortality occurred (Fig. 2), *Gremmeniella* was the main killing agent (74.6% of mortality in the NE subsample and 63.2% in the SW site; Fig. 3), followed by *Phacidium* (6.8% of mortality in the NE subsample and 1.7% in the SW site; Fig. 3). Only 10% of the trees infected by *Gremmeniella* survived, while 19% of the trees infected by *Phacidium* survived. Subsequent mortality after infection by the fungi took 3.3 ± 2.8 yr after *Gremmeniella* infection and 2.2 ± 1.9 yr after *Phacidium* infection. *Gremmeniella* and *Phacidium* occurred together less frequently than expected by chance ($\chi^2_{[24]} = 3.4$, $P < 0.01$). The
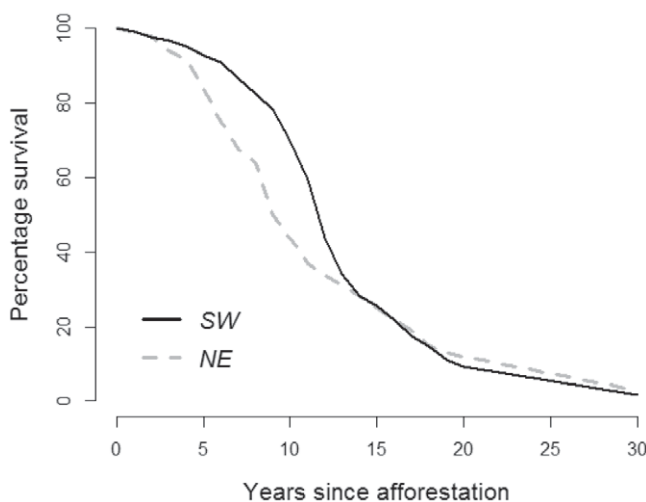
FIGURE 2. Survival curves for *P. cembra* for the period 1975–2005 for the subsample of the Northeast (NE) plantation and for the Southwest (SW) plantation. For each site, survival is expressed as a percentage of the 550 trees planted as seedlings.

major *Gremmeniella* outbreaks occurred between 1984 and 1988; after 1988, the infection rate stayed relatively constant with a slight increase after 1991 at the NE site (Fig. 3). Our results indicate that high rainfall and low temperatures (high GIV) during the growing season favor fungi spread and subsequent outbreak; in 1984, the GIV for September (end of the growing season) was almost double that of any other year of the 20-year period examined. In 1985, the infection on the NE site increased fivefold and the infection at the SE site threefold (Fig. 3). The GIV for the month of June (start of the growing season) was between 1.5 and 5 times higher in 1986 than in any other year of the 20-year period studied. On the other hand, the GIV values for July and August showed very little interannual variation. The relationships between snowmelt date and maximum snow depth and the following years' infection by *Gremmeniella* or by *Phacidium* were not significant (linear regression, $P > 0.05$).

The initial date of snowmelt in spring was the most important factor for predicting the spatial pattern of infection of both fungi at the NE site, as identified by the DTs where this variable always represented the first or second split over the first 10 years (Figs. 4 and 5; Appendix Figs. A3 and A4). Ten years after planting (1985), infection by *Gremmeniella* was higher than 40% in areas where the snowmelt date was later than day 143 (23 May; Fig. 4) and higher than 50% in areas where snowmelt date was later than day 147 (27 May; Fig. 4), with the highest infection rate for trees above 2128 m (more than 70% infected). Snowmelt date was also the most critical factor for *Phacidium* infection but with opposite effect. The highest infection rate by *Phacidium* in 1985 occurred in areas where snowmelt date was earlier than day 130 (10 May; 18% infected; Fig. 5), and was lower than 5% in the areas where snow disappeared after day 143 (23 May). The proportion of trees infected by *Phacidium* was consistently higher at North exposures and Ridges than at East exposures and Gullies (Fig. 5, Appendix Figs. A3 and A4). Wind was marginally important (i.e. last split of the DTs) during the first 7 years of the planting, with higher rates of infection of *Gremmeniella* and *Phacidium* in areas with higher wind (Appendix Fig. A3, part b, and Fig. A4, part a), but it was not a significant factor for infection in 1985.

In 1985, the planted *P. cembra* trees infected by *Gremmeniella* occurred within 40 m of the mature *P. cembra* trees less frequently than expected at random (Fig. 6, part b; the same pattern is observed in 1979 and 1982, so results are not shown). In contrast, trees infected by *Phacidium* showed a significant positive spatial association with the mature pine trees to distances within 75 m in 1985 (Fig. 6, part a; the same pattern is observed in 1979 and 1982, so results are not shown). The final spatial pattern of surviving trees at the NE site in 2010 largely matches the pattern of the mature remaining *P. cembra* trees (Fig. 1).

Discussion

Our results did not support the hypothesis that mortality caused by snow fungi should be higher in the NE aspect than in the SW aspect. At both plantations, only ca. 5% of *P. cembra* trees survived 30 years after planting. We found that the main causes of mortality at both plantations were snow fungi. In our study, the plantations belong to an even-aged cohort, and thus all individuals go through the same critical life stage at the same time, certainly
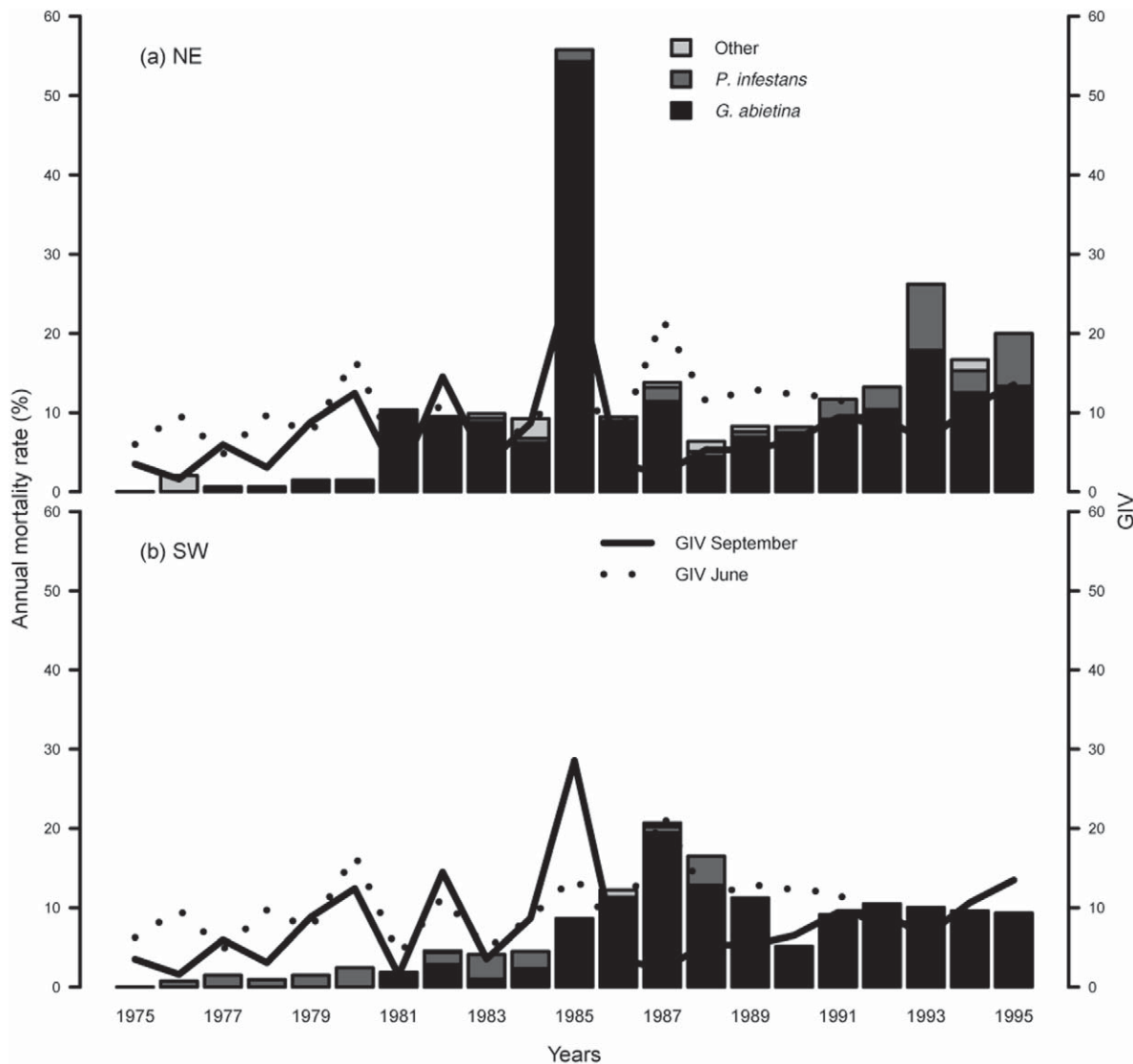
FIGURE 3. Annual mortality rates for *P. cembra* for the period 1975–1995 caused by *Gremmeniella*, *Phacidium*, and other causes (mainly attributed to competition from herbaceous vegetation at the NE site and drought at the SW site) at: (a) the subsample area of the NE afforestation and (b) at the SW afforestation. Annual mortality rates are calculated by treating the number of trees alive in the previous year as 100%. The *Gremmeniella* index value (GIV) for June and for September are represented in each graph as a line; GIV is lagged by one year to facilitate the interpretation, and index values are divided by two for ease of representation.

yielding higher mortality rates than in a natural setting where we would probably find a more diverse tree demography. Moreover, the plantations result in an unnatural tree distribution, since Eurasian nutcrackers generally target sites with smaller accumulation of snow such as ridges, slopes, and rock ledges (Tranquillini, 1979). However, a recent analysis of the expansion of *P. cembra* above treeline during the last 30 years on both sides of the valley shows that seedlings are not restricted to these favorable microsites (Leibold, 2012).

Our plantation study provides data on the spatial spread of infection and on annual mortality. To our knowledge, our study provides the first evidence for a major influence of snow fungi on mortality at treeline in snow-rich regions such as the Alps. However, additional evidence from different geographic locations and more natural tree distribution in the Alps, including north and south

aspects, would be necessary before the conclusions drawn from our experimental plantations can be generalized. Furthermore, our results suggest that snow fungi could be one of the mechanisms explaining the limited upward shift potential of certain treeline species after grazing cessation in the 20th century (Grace et al., 2002; Gehrig-Fasel et al., 2007), and that in addition to other factors such as browsing (e.g. Speed et al., 2010), snow fungi could prevent the treeline upward expansion predicted under future climate change scenarios (e.g., Dullinger et al., 2004). The influence of snow fungi at broad scales was already suspected in an observational field study of four moraines in northern Sweden (Stöcklin and Körner, 1999), but the source of mortality was confounded by the combined effect of browsing and pathogen damage. Snow fungi were potentially responsible for large-scale mortality at the Arctic treeline of eastern Canada (Auger and Payette, 2010), but no con-
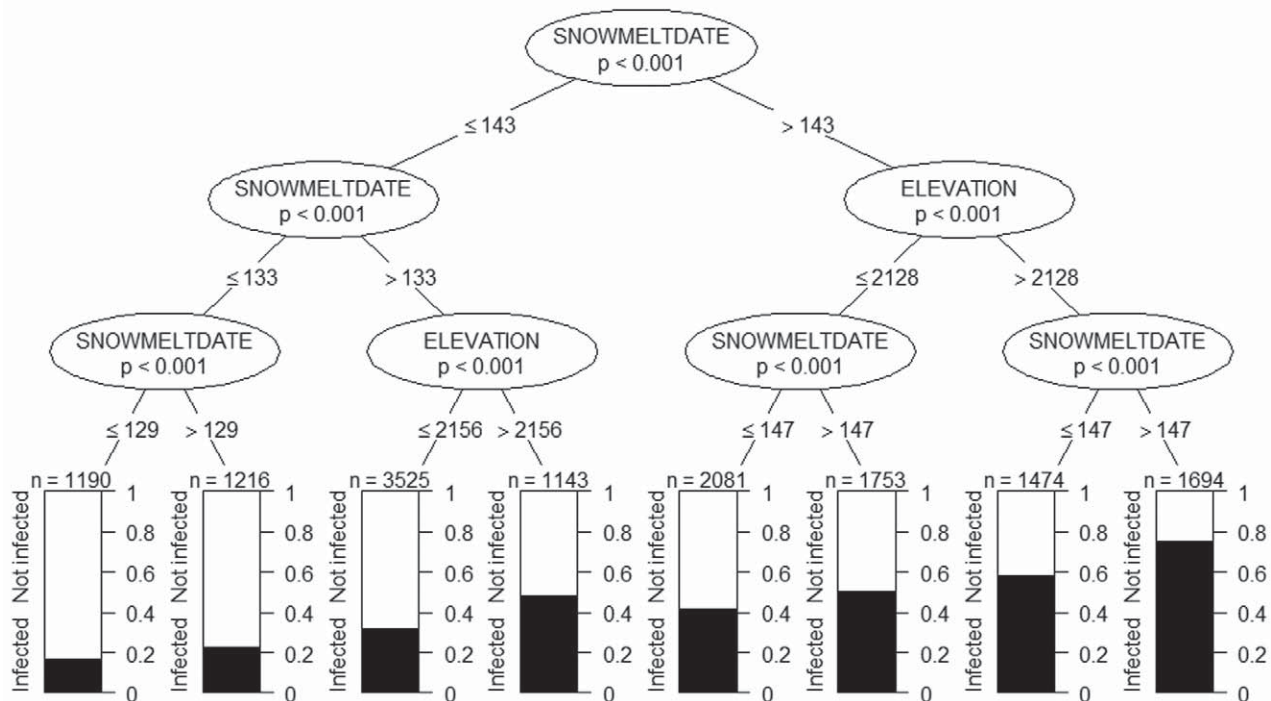
Infection by Gremmeniella in 1985

FIGURE 4. Decision tree for infection by *Gremmeniella* in 1985 at the NE site (10 years after planting). The relative frequencies of both response classes are shown in the bottom nodes of the classification tree (the proportion of infected trees is shown in black, and the proportion of uninfected trees is shown in white). Snowmelt date is expressed in days where day 1 is 1 January.

trolled field study was available to test this hypothesis. Furthermore, regional-scale studies in the Rocky Mountains showed the effect of the invasive blister rust in reducing the occurrence of *Pinus albicaulis* treeline (Resler and Tomback, 2008; Smith et al., 2011), indicating the importance that fungi can have on the decline of five-needled pines at large scales. Our results together with previous studies (see also Wardle, 1968; Senn, 1999; Zhong and Van der Kamp, 1999; Cunningham et al., 2006; Kullman, 2007) provide strong evidence that fungal infection is a major cause of tree mortality at sapling stages, thereby influencing treeline's structure and species composition.

Our analysis of the *P. cembra* plantations showed that the spatial patterns of mortality by snow fungi are largely a result of the patterns of snowmelt timing as we had hypothesized. Although Senn (1999) showed the dependence of snow fungi infection and spread on snow duration, we found that increased snow cover duration by 10 days almost doubled pine infection and subsequent mortality by *Gremmeniella*. The infection rate of *Gremmeniella* in 1985 was as high as 75% above 2130 m elevation in the areas where the snowmelt date was later than day 147 (27 May). Similarly, Barbeito et al. (2012) found that mortality in *P. cembra* seedlings increased sharply above 2160 m elevation for the period 1975–2005. On the SW aspect, snow data per plot were not available, but average snow disappearance date was 15 May (day 135; Schönenberger and Frey, 1988); given the elevation of the SW site (>2156 m), this would correspond to an infection by *Gremmeniella* of ca. 50% at the NE site in 1985 (Fig. 2). Thus, a combination of snow cover duration and elevation was likely an important environ-

mental factor influencing *Gremmeniella* infection at the SW site, too. Similarly, other experiments indicate a relationship between snow duration and snow fungi infection such as *Picea abies* saplings (15–20 cm tall infected by *Herpotrichia juniperi*, Swiss Alps (Cunningham et al., 2006); and for the dwarf shrub *Empetrum hermaphroditum* in Sweden infected by *Arwidssonia empetri* (Olofsson et al., 2011).

Infection and subsequent mortality of *P. cembra* by *Phacidium* at the NE site occurred mainly on the ridges, which had earlier snowmelt in spring. The mature trees were naturally established on ridges due to seed dispersal by the Eurasian nutcracker (e.g., Holtmeier, 1966). These results suggest that *Phacidium* plays a major role in places with earlier snowmelt and attacks vigorous plants (Roll-Hansen, 1989). At the natural treeline, ca. 65% of the trees infected by *Phacidium* were located on the ridges at both NE and SE slopes (*n* = 410 trees; results not shown).The proximity of the mature *P. cembra* trees to the planted trees at the NE site together with the very low infection of the planted trees by *Phacidium* at the SW site (1.7%), where the closest mature *P. cembra* trees were 40 m away from the planted trees, suggest that the pattern of *Phacidium* infection is partly a result of direct branch-to-branch contact (e.g., Burdon et al., 1992). Moreover, mature Swiss stone pines could have enhanced *Phacidium* infection by increasing the snow accumulation around them, as observed by Holtmeier (1966) in the Upper Engadine (Switzerland). Similarly, ''ribbon forests'' (i.e. elongated tree islands), which produce leeward snow drift, could also facilitate tree infection by *Phacidium* (Bekker and Malanson, 2008). Regardless of mechanism, our results show that
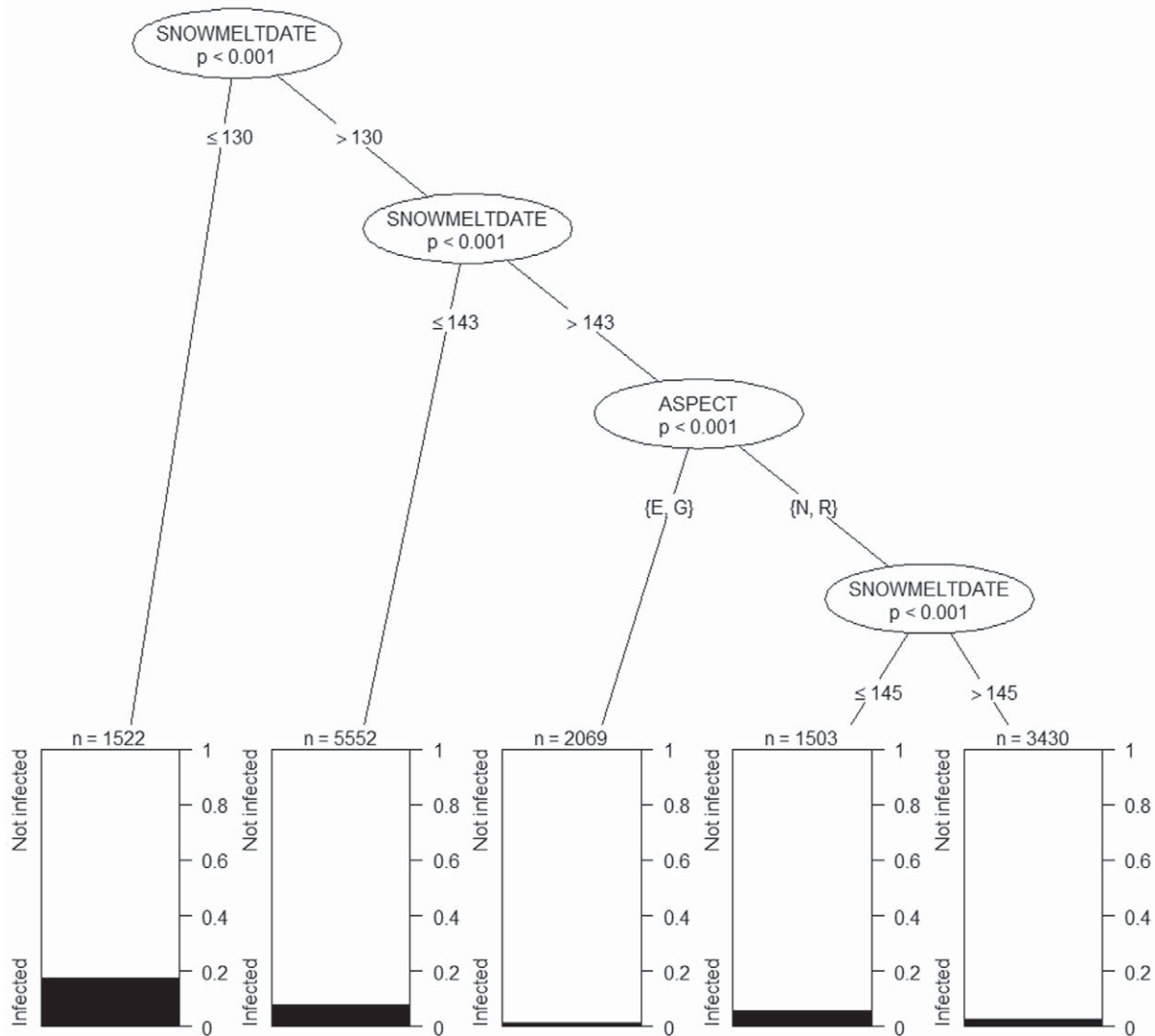
FIGURE 5. Decision tree for infection by *Phacidium* in 1985 at the NE site (10 years after planting). The relative frequencies of both response classes are shown in the bottom nodes of the classification tree (the proportion of infected trees is shown in black, and the proportion of uninfected trees is shown in white). Aspect is classified in Gully (G), Ridge (R), North (N), and East (E) exposures. Snowmelt date is expressed in days where day 1 is 1 January.

Phacidium infects trees on the most favorable sites for the survival of *P. cembra* to *Gremmeniella* attacks, and thus it controls tree density. This is consistent with the commonly observed scattered treeline pattern in the Alps (e.g., Lingua et al., 2008).

The highest percentage of pine trees were killed during the first 10–15 years. Cold and wet growing seasons during 1983–1984 and 1987 probably provided good conditions for sporulation, for spreading of spores by a water splash mechanism, and for infection of the fungi at our study site. Similar conditions during the growing season preceded extensive mortality by *Gremmeniella* in *P. contorta* plantations and in *P. sylvestris* in northern Sweden, Finland, and Denmark (Karlman et al., 1994; Hellgren and Barklund, 1992; Nevalainen, 1999; Thomsen, 2009). Values of GIV above 10 were reported to precede fungi outbreaks (e.g. Thomsen, 2009). At our sites, a higher value of GIV was found to trigger *Gremmeniella*

outbreaks. A cold and rainy September in 1984 resulted in a high GIV (above 20), which triggered the largest infection rate by *Gremmeniella* at the NE site. Similarly, high GIV values in June 1986 (again above 20) were found before years of high infection at both the NE and SW sites. These results confirm the importance of the weather conditions at the beginning and the end of the growing season for snow fungi spread, in addition to the existence of trees in an age range susceptible to attacks (Thomsen, 2009).

We found that small variation in the spatial patterns of snowmelt resulted in large differences in mortality, while the temporal variability in snow—represented by the maximum snow depth of the previous winter—did not play a significant role in *Gremmeniella* and *Phacidium* infections. *Gremmeniella* is more successful in trees that are stressed by adverse environmental conditions (Senn, 1999), and thus inter-annual differences in snowmelt dates among
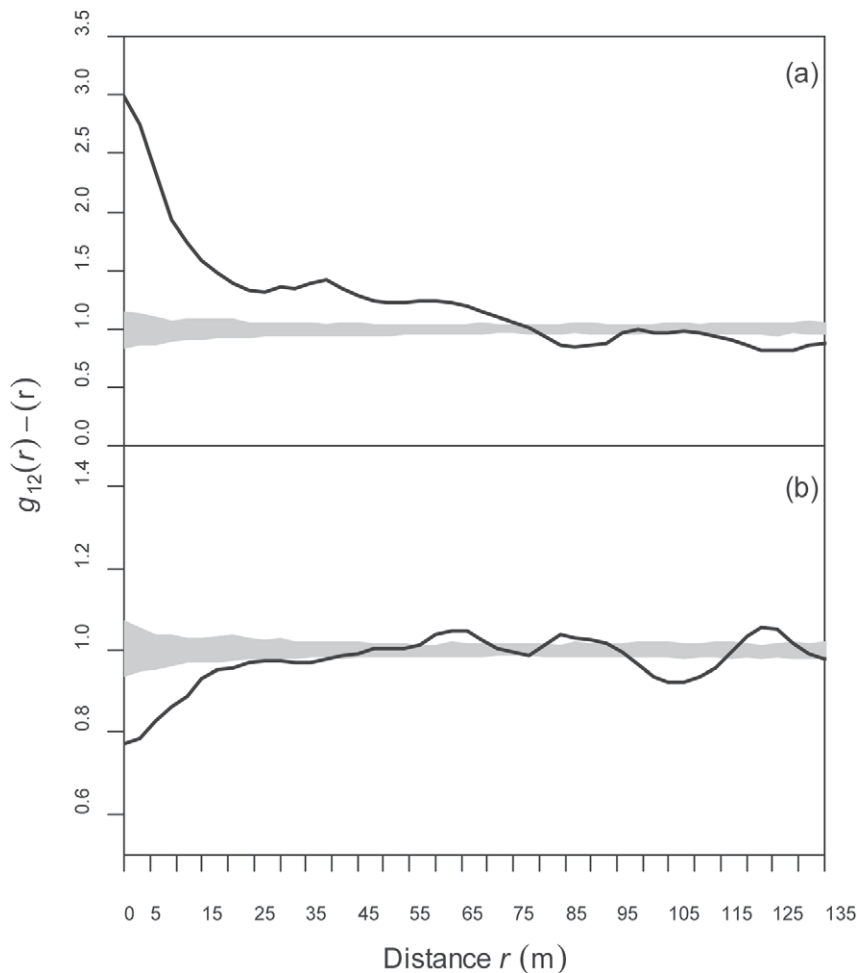
FIGURE 6. Bivariate point-pattern analyses of mature versus planted *P. cembra* trees in 1985 in the NE plantation infected by (a) *Phacidium* and (b) *Gremmeniella*. The calculated $g_{12}(r)$ (solid black line) values above the 95% CI bands corresponding to the antecedent condition null model (in light gray) indicate a positive association between mature and planted trees. Values of $g_{12}(r)$ below the CI bands indicate negative association.

sites (i.e. the spatial pattern of snow which remains stable over time) are likely more important than the difference within sites over time. The lack of correlation between snow depth and *Phacidium* infection strengthens the hypothesis that the infection's spread is governed by density-dependent interactions.

Results of other seedling planting studies in the Swiss Alps suggested that the current altitudinal range of *P. cembra* is not primarily controlled by temperature (Hättenschwiler and Körner, 1995; Zurbriggen et al., 2013). Our findings support these results and suggest that changes in treeline dynamics cannot be simply predicted from changes in temperature patterns alone and that other interactions, including date of snowmelt, have to be considered. Our results show that one or two years with extremely cold and wet growing seasons (1984 and 1986) within a 20-year period were enough to trigger large *Gremmeniella* outbreaks. Nevertheless, even if *Gremmeniella* is currently the main killing agent of *P. cembra* above treeline, it is possible that competition between the two fungi influences their relative occurrence (McBeath, 2002). This interaction at our study site may explain the limited presence of *Phacidium* in years of the most widespread *Gremeniella* attacks (Fig. 3), and almost no overlap in their spatial pattern (Fig. 6). Therefore, *Phacidium* may gain importance if *Gremmeniella* is limited by abiotic factors (i.e. in case of an earlier snowmelt) or if tree density (and therefore snow accumulation around mature trees) increases as detected in other treelines (e.g. Kullman, 2002).

Conclusions

This study, based on two different slope exposures, provides evidence that snow fungi can be a major cause of mortality above the current treeline. Within a given elevation, *P. cembra* treeline was strongly influenced by snow fungi associated with the spatial pattern of snow duration. Our study provides experimental evidence of the dramatic effects that even moderate changes in the duration of snow cover can have for sapling tree–pathogen interactions at treeline. One or two growing seasons with extremely high ratios of rainfall to temperature can cause severe infection by *Gremmeniella* during the time that trees are below snow cover (i.e., more than 30 years at the elevation studied), and after these infection events, the snow cover largely determines the mortality pattern. Although *Gremeniella* was the major mortality agent in our study, an earlier snowmelt would favor higher rates of infection by *Phacidium*. Therefore, under future climatic scenarios, the latter may prevail. Consequently, changes on snow fungi activity through shifts in the initial timing of snowmelt, potentially due to climate change, can be as important for alpine treeline community development as the direct effect of increasing temperatures. A better understanding of the frequency and magnitude of the infection by snow fungi can provide critical information for incorporating outbreaks into models simulating treeline response to climate, and towards understanding how treeline position and species composition will respond to climate warming.

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Acknowledgments

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APPENDIX

FIGURE A1. Location of the two plantation research sites on both sides of the Dischma Valley in the central Alps, Switzerland (photograph by Foto Furer).

FIGURE A2. *P. cembra* **trees affected by snow fungi at the NE site, (a)** *Phacidium infestans* **and (b)** *Gremmeniella abietina* **(photographs by R. L. Brücker).**
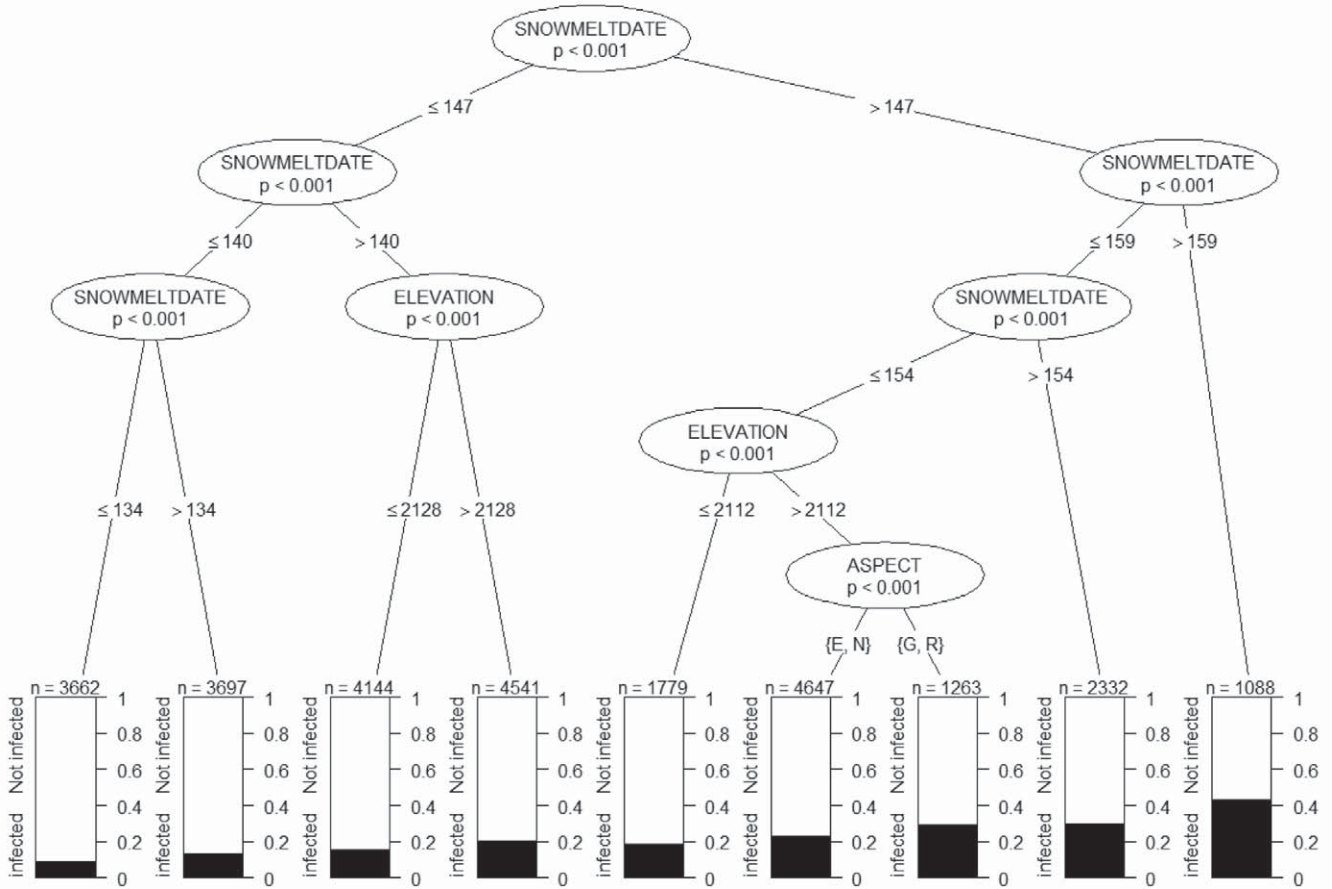
FIGURE A3. (a) Decision tree for infection in 1979 at the NE site (4 years after planting), by *Gremmeniella*. The relative frequencies of both response classes are shown in the bottom nodes of the classification tree (the proportion of infected trees is shown in black, and the proportion of non-infected trees is shown in white).
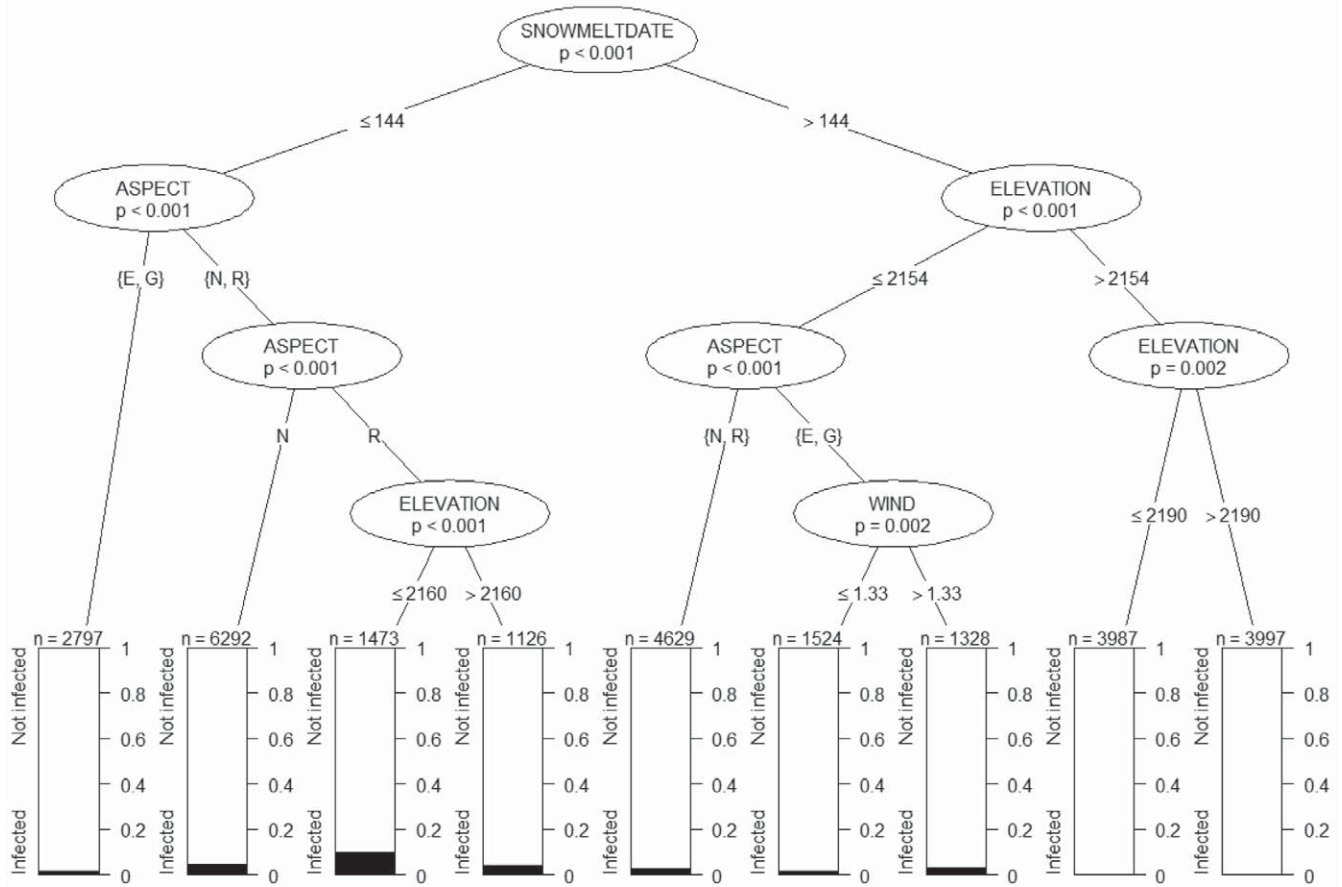
FIGURE A3. (cont.) (b) Decision tree for infection in 1979 at the NE site (4 years after planting), by *Phacidium.* The relative frequencies of both response classes are shown in the bottom nodes of the classification tree (the proportion of infected trees is shown in black, and the proportion of non-infected trees is shown in white).
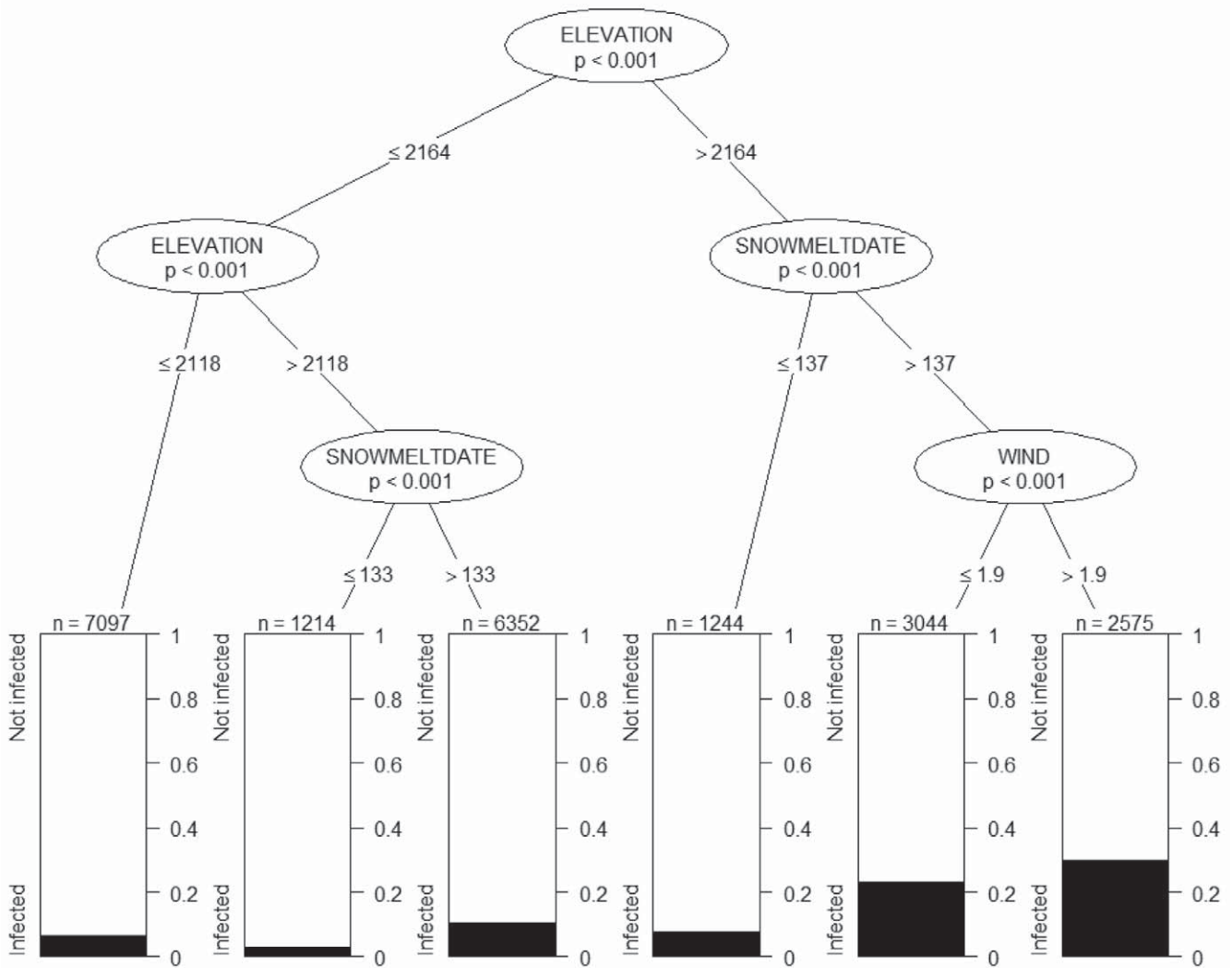
FIGURE A4. (a) Decision tree for infection in 1982 at the NE site (7 years after planting), by _Gremmeniella_. The relative frequencies of both response classes are shown in the bottom nodes of the classification tree (the proportion of infected trees is shown in black, and the proportion of not infected trees is shown in white).
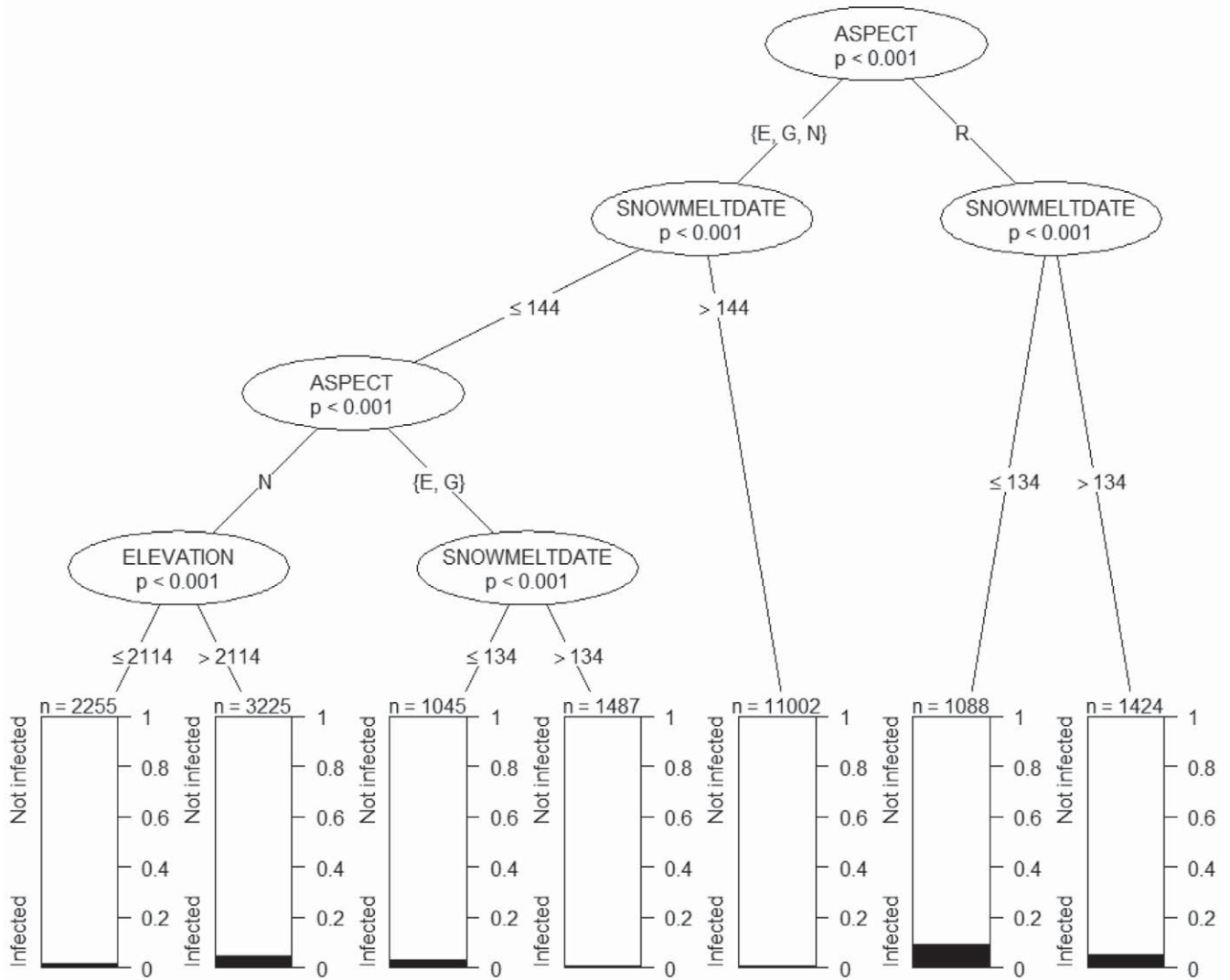
FIGURE A4. (cont.) (b) Decision tree for infection in 1982 at the NE site (7 years after planting), by *Phacidium*. The relative frequencies of both response classes are shown in the bottom nodes of the classification tree (the proportion of infected trees is shown in black, and the proportion of not infected trees is shown in white).