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Current and future conifer seed production in the Alps: testing weather factors as cues behind masting

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Abstract
Temporal patterns of masting in conifer species is an intriguing phenomena that has cascading effects on different trophic levels in ecosystems. Many studies suggest that meteorological cues (changes in temperature and precipitation) affect variation in seed-crop size over years. We monitored cone crops of six conifer species in the Italian Alps (1999-2013) and analysed which seasonal weather factors affected annual variation in cone production at forest-community level. Larch, Norway spruce and silver fir showed masting while temporal patterns in *Pinus* sp. were less pronounced. We found limited support for the temperature difference model proposed by Kelly et al. Both seasonal (mainly spring and summer) temperatures and precipitations of one and two years prior to seed maturation affected cone-crop size, with no significant effect of previous year's cone-crop. Next, we estimated future forest cone production until 2100, applying climate projection (using RCP 8.5 scenario) to the weather model that best predicted variation in measured cone-crops. We found no evidence of long-term changes in average cone production over the 21st century, despite increase in average temperature and decrease in precipitation. The amplitude of predicted annual fluctuations in cone production varies over time, depending on study area. The opposite signs of temperature effects one and two years prior to seed set show that temperature differences are indeed a relevant cue. Hence predicted patterns of masting followed by one or more years of poor-medium cone production suggest a high degree of resilience of alpine conifer forests under global warming scenario.

Keywords
Global warming; Alps; Conifer; Forest; Cones; Masting

1 Introduction

Seed production of several forest tree species varies widely from year to year (Kelly 1994; Kelly and Sork 2002; Broome et al. 2007; La Montagne and Boutin 2007; Wesolowksi et al. 2015). For example conifer cone (seed) crops can vary from extremes of no cones to very high production, called "masting" (Kelly and Sork 2002; Salmaso et al. 2009; Krebs et al. 2012). Many studies and theories focused on masting patterns and on the factors involved in this phenomenon. Two of the most well known hypotheses are "predator satiation" (Janzen 1971) and "pollination efficiency" (Kelly 2001). Both theories highlight the fact that for plants, especially for those living in scarcely productive habitats, it is convenient to accumulate resources until they can produce a great amount of seeds in specific occasions, to enhance reproductive success (Kelly and Sork 2002). This type of plant "behaviour" is very important for forest management and ecosystem equilibrium, and both human (Broome et al. 2007) and animal populations (Boutin et al. 2006; Wauters et al. 2007, 2008; Fletcher et al. 2010; Zong et al. 2012) adapt their activities and reproductive strategies according to this pulsing phenomenon.

The part of this ecological mechanism that is still not entirely verified is the cause driving synchronous masting over large areas and plant populations and the factors determining the interval between masting events. One of the mechanisms investigated is pollen coupling (Satake and Iwasa 2000; Crone and Rapp 2014): if plants produce flowers in a low-flowering year, there will be little fertilization and consequently few plant resources will be allocated for seed production. This low-energy need will allow plant to store enough resources to invest in reproduction the following years. On the other hand, during high-flowering years, plants will be easily pollinated producing larger amount of seeds, which will, however, result in greater depletion of stored resources. The two faces of this mechanism facilitate plants synchronisation. Synchronization of different species is instead often explained by assuming that the above mentioned phenological processes in these species respond to a common environmental cue such as climate conditions (the "weather as a cue" hypothesis e.g. Kelly et al. 2013; Pearse et al. 2014). However, the "weather as a proximate driver" hypothesis suggests even that weather factors, mainly temperature and precipitation, are actually the drivers affecting either flower production, pollination success or maturation of pollinated flowers into seeds (e.g. Koenig and Knops 2013; Pearse et al. 2014). In this context, it becomes important to understand the effect of global warming on masting plants (Lindner et al. 2010). In the 21st century, CO_2 levels are expected to further increase and, as a consequence, most scenarios predict a temperature increase of up to 4-5 °C by 2100, both in Mediterranean ecosystems and in Arctic and Alpine regions (IPCC 2013).

Forest trees have a long life span, from several decades to over a century, and changes in climate conditions can significantly affect these species (LaDeau and Clark 2001; Lindner et al. 2010). Several authors analysed the relation between weather and masting, finding different weather cues (Juday et al. 2003; Krebs et al. 2012; Kelly et al. 2013; Roland et al. 2014). Among factors tested, temperature, in particular summer temperatures one and two years before seed maturation, seems to be the most important weather variables affecting production and synchronisation of seed crops (Kelly et al. 2013; Roland et al. 2014). Most of the studies have been carried out on single species

(Mencuccini et al. 1995; Pelfini et al. 2006; Crone et al. 2011; Krebs et al. 2012; Walker et al. 2012; Roland et al. 2014), but in montane and subalpine mixed conifer forests, all tree species must be considered to better understand the ecosystem reaction to global warming. In the present study we monitored cone crops of six conifer species in the Italian Alps from 1999 to 2013. Our first aim was to test different climate-cone models to explore which model best explained the observed annual variation in cone production over the 15-year study period. In a first step, we tested the temperature-difference (ΔT) model proposed by Kelly et al. (2013) for each species separately and then compared it with a model which contained the summer temperatures of one and two years before cone counts, and repeated this using summer temperatures of the same year and one year before cone counts (see also Pearse et al. 2014). Next we investigated to what extend the model proposed by Kelly et al (2013) could explain variation in conifer seed production for all species combined. Since previous studies on conifer cone production showed that also other weather factors were correlated to variation in seed-crop size (e.g. Juday et al. 2003; Krebs et al. 2012; Roland et al. 2014), we also investigated a series of models which analysed the influence of several seasonal climate factors, such as temperature and precipitation in the same year and in the two years preceding cone production, for the entire dataset comprising all conifer species. All these models were tested with and without the seed-crop size of the previous year to take into account potential constraints of resource limitation resulting from the previous year's seed set on current seed-crops (Sala et al. 2012; Pearse et al. 2014).

Our second aim was to estimate trends and variability in future conifer cone production due to global warming, starting from our model that best explained the observed variation in the collected data, using projections from climate models. Hence, our aim was not to construct the best possible model testing many detailed weather parameters, as for example short-time extreme weather events, since such events are not available for climate change scenarios (Zwiers et al. 2013). In contrast, we wanted to explore which is the best model fitting our current seed-crop size data using only those weather variables (seasonal temperature and precipitation) that can be predicted with a certain degree of reliability in future climate change scenarios (Maslin and Austin 2012).

2 Materials and methods

2.1 Study area

We monitored cone production in 7 study areas within mature, secondary montane and sub-alpine mixed conifer forests in the Italian Alps (age of mature trees between 70 and 120 years-old), with elevations ranging from 1100 to 2100 m a.s.l. (the upper timber-line, Table 1). Five of them were located in Central Alps, Lombardy region and two in Western Alps, Valle d'Aosta region. In Lombardy, four of the areas were inside the Stelvio National Park, and both sites in Valle d'Aosta were inside the Gran Paradiso National Park (Figure 1). Our study areas are independent sampling plots within the 3056 square kilometers of coniferous forests for Central-Western Italian Alps (CORINE Land Cover Level IV codes 3122: 297 km^2, 3123: 1589 km^2, 3124: 1170 km^2, ISPRA, 2010).

The proportion of different conifer species varied among study areas and, in some cases, also at a fine-grained level within some of the study areas (Wauters et al. 2008; Salmaso et al. 2009; Rodrigues et al. 2010). We determined forest composition by establishing 20 x 20 m (400 m^2) vegetation sampling plots (VSP) across the study area (n = 20 to 30) (Salmaso et al. 2009; Romeo et al. 2010; Zong et al. 2010). The VSPs, were placed on a 150 x 150 m grid (areas CED, CAN, COG, RHE) or were randomly distributed over the study area (areas OGA, VAL, BOR). In each VSP we counted the number of mature trees of each species and two mature trees (hereafter called "sample trees") per species were chosen randomly amongst trees with an easily visible canopy for counting cones and measuring the average diameter at breast height (DBH) (Salmaso et al. 2009; Rodrigues et al. 2010).

Table 1. Characteristics of the study area. Pc: *Pinus cembra*; Ld: *Larix decidua*; Pa: *Picea abies*; Pm: *Pinus mugo*; Aa: *Abies alba*; Pa: *Picea abies*; Fs: *Fagus sylvatica*; Ps: *Pinus sylvestris*. Remaining difference to 100%: dead trees.

Study area	**Elevation (m a.s.l)**	**Number of sample trees**	**Trees species %**	**Tree density (trees/ha)**	**Period cones counts**
Bormio	1950 – 2130	40 Pc; 40 Ld; 40 Pa;	77 Pc; 13 Ld; 8 Pa	633	2001 – 2012
Cancano	1940 - 1970	40 Pm	100 Pm	3308	2006-2012
Cedrasco	950 – 1450	30 Ab; 40Pa; 3 Ps; 8 Ld;	43 Aa; 39 Pa; 3 Ps; 3 Ld; 11 Fs	720	1999 – 2009
Oga	1250 – 1450	38 Ps; 28 Pa; 10 Ld	88 Ps; 9 Pa 3 Ld	789	1999-2005
Valfurva	1650 – 1870	40 Pa; 18 Pc; 4 Ld	89 Pa; 6 Pc; 2 Ld	464	2001-2012
Cogne	1550-1860	47 Pa; 58 Ld	45 Pa; 54 Ld	894	1999-2013
Rhemes	1660-1970	60 Pa; 48Ld	85 Pa; 11 Ld	773	1999-2008

2.2 Cone counts

Each year in August we counted the fresh cones in the canopy of all conifer sample trees from a fixed position using 10 x 40 binoculars (for details see Wauters et al. 2005 and Salmaso et al. 2009). Overall, the number of cones has been recorded from 1999 to 2013, but periods differed among study areas (Table 1).

2.3 Observed climate data

Since a dedicated meteorological station for each study area was not available, we collected data from 15 different meteorological stations in the proximity of each area (Figure 1), obtaining climate time series data from the local authorities operating the regional meteorological station networks in Valle d'Aosta and Lombardy (ARPA Lombardia 2014; Centro Funzionale Regionale Regione Autonoma Valle d'Aosta 2014). We used daily average temperature and cumulated daily precipitation data. To avoid confusion between abbreviations for time and for temperature we used t for time (current year = $year_t$) and T for temperature in °C being aware we are not using absolute temperature in Kelvin. Correlations between meteorological stations were tested daily, monthly and seasonally; hereinafter we only use seasonal data. According to correlation tests for neighbouring groups of meteorological stations (9-14 years of data), both seasonal temperature (all correlation coefficients $r > 0.96$) and seasonal precipitation (all correlation coefficients $r > 0.50$) data were pooled: to account for local variations, series from each station were standardized and then averaged, yielding a single temperature and precipitation series for each study area. These transformations allowed us to avoid the problem of missing data in single-station climate time series (due to differences in the period of operation of the different stations, or to random, unpredictable station sensor failures) and to create a complete and continuous dataset.
Because of the large spatial scale (about 40 km) of climate projection model outputs (next section), the meteorological station datasets were averaged into 3 main "meteorological macro-areas" (AVA: Alta Valtellina; BAV: Bassa Valtellina; VDA: Valle d'Aosta; see Table 2 for details). All further analyses were carried out for each of these three macro-areas.

Table 2. Averaged meteo area.

Meteoreological macro-area	**Study Area**	**Meteorological Station**
AVA (Alta Valtellina)	Oga, Bormio, Cancano and Valfurva	Bormio; Valdidentro – Cancano; Valfurva – S.Caterina Valfurva
BAV (Bassa Valtellina)	Cedrasco	Caiolo; Carona – Carisole; Foppolo

VDA (Valle d'Aosta)	Cogne and Rhemes	COCRE; COLIL; COVAL; RHCAP; RHCHD; RHCHV; RHPON; VSEAR; VSMOL

2.4 Climate variable selection

We selected climate variables proposed by Kelly et al. (2013): summer temperatures of the same year (t), the previous year (t-1) and of two years before seed set (t-2) and the temperature difference between same and previous year (ΔT1) and temperature difference between one and two year prior to seed set (ΔT2). Then we selected climate variables within seasons that are linked to conifer phenology (e.g. Selås et al. 2002): average of mean daily temperature and cumulated daily precipitation in winter (December to March), spring (April to June) and summer (July to August). Winter climate was only considered for the winter preceding the cone-crop since this winter's severity and winter drying could cause flower bud mortality and severe plant damage (Johnson et al. 1986; Inouye 2000; Man et al. 2013). Based on previous studies on conifers and bud and seed phenology (Krebs et al. 2012; Tranquillini et al. 2012; Kelly et al. 2013; Roland et al. 2014), we considered spring and summer climate for the year of cone production (t), the previous year (t-1) and two years before seed maturation (t-2). By considering seasonally-aggregated summary statistics, a total of 14 different climate variables were produced (Table 3). Finally, we added also cone production of the previous year, based on theories of trees depleting energy resources after a mast crop (Kelly et al. 2002). Moreover to verify the suggestions of Kelly et al. (2013) and Pearse et al. (2014) to incorporate ΔT also in more complex models with other variables, we calculated ΔT1 and ΔT2 for all seasonal temperatures previously selected (Table 3).

Table 3. Climate variables tested in the full model and their abbreviation. ΔT1: T of year $_{t}$ – T of year $_{t-1}$; ΔT2: T of year $_{t-1}$ – T of year $_{t-2}$

Climate variables	**Abbreviation**	**Climate variables with ΔT**	**Abbreviation**
Summer temperature	SuT	Summer ΔT1 Summer ΔT2	SuDT SuDT2
Summer temperature of year $_{t-1}$	SuT-1		
Summer temperature of year $_{t-2}$	SuT-2		
Spring temperature	SpT	Spring ΔT1 Spring ΔT2	SpDT SpDT2
Spring temperature of year $_{t-1}$	SpT-1		
Spring temperature of year $_{t-2}$	SpT-2		
Winter temperature	WiT	Winter ΔT1	WiDT
Summer precipitation	SuP	Summer precipitation	SuP
Spring precipitation	SpP	Spring precipitation	SpP
Winter precipitation	WiP	Winter precipitation	WiP
Summer precipitation of year t-1	SuP-1	Summer precipitation of year $_{t-1}$	SuP-1

Spring precipitation of year $_{t-1}$	SpP-1	Spring precipitation of year $_{t-1}$	SpP-1
Summer precipitation of year $_{t-2}$	SuP-2	Summer precipitation of year $_{t-2}$	SuP-2
Spring precipitation of year $_{t-2}$	SpP-2	Spring precipitation of year $_{t-2}$	SpP-2

2.5 Climate projections

Present-day and future climate projections are provided by simulations with the regional climate model (RCM) RegCM4, run by ICTP (International Centre for Theoretical Physics Abdus Salam) in the framework of the Med-CORDEX (Mediterranean-COordinated Regional climate Downscaling Experiment) initiative (http://www.medcordex.eu/) and collected for the NextDATA project (http://www.nextdataproject.it/). Daily precipitation and minimum and maximum temperature data are available for the period 1971-2005 (historical run) and for the period 2006-2100 (in the RCP8.5 scenario) at a spatial resolution of 0.44° (between 35 and 48 km).
The RegCM4 model, evaluated during the historical period, shows reasonable skill in reproducing the spatial climatological pattern of different precipitation and temperature indices. However, climate model can have systematic biases that may reduce their applicability for impact assessment models. To this end the precipitation data for the study area were bias-corrected scaling the simulation by the ratio of the observed and simulated mean in the training period (see Teutschbein and Seibert 2012 for a discussion of the method). Temperature data were bias-corrected adding to the daily RCM simulation data the mean difference between the observations and the simulation in the historical period (1971-2005).
The data were validated and bias-corrected considering, for temperature, the high-resolution dataset of interpolated observations EOBS version 10.0 (Haylock et al. 2008). This dataset interpolates daily temperature data from quality-controlled stations over a regular grid at 0.44° resolution; data are available for the period 1950-2013 (see http://eca.knmi.nl/ for more details).
The observed precipitation data used to calibrate the model data are provided by the recently developed gridded dataset EURO4M-APGD (Isotta et al. 2014) available at a resolution of about 5 km for the period 1971-2008. To compare the simulations with the observations, we applied an up-scaling process to the EURO4M-APGD grid at 0.44° resolution by means of an interpolation process. This consisted in (i) bilinearly interpolating the original data to a 1 km scale, then (ii) aggregating these series at 0.44° resolution averaging the 1 km points that fall in each 0.44° grid cell. The bias corrected outputs (at 0.44°) are available at the web page of the NextData project (http: //www.nextdataproject.it/) in standard netcdf format.
For the present study, data were seasonally aggregated and standardised (see section 2.3). This new dataset was then used to project the cone production model estimated from the measured data of cone counts and from observed climate variables, to estimate cone production until the end of the 21st century.

2.6 Statistical analyses

Each yearly time series of cone counts was first tested for autocorrelation using an autoregressive model to verify if there was a pattern in masting behaviour of different species in different study sites.
Climate independent variables were standardised as follow:
$\mathbf{(WF_{d,s}-mean(WF_s))/\sigma_s}$, where *WF*=climate variable, *d*=day, *s*=meteo station, σ = standard deviation.

The various conifer tree species have different overall average and range of cones produced per tree (e.g. Salmaso et al. 2009; Wauters unpubl. data) making it difficult to combine data of direct cone counts for different species in a forest type (study area). Therefore, and since we were mainly interested in studying the annual variation in overall forest seed production and not species-specific estimates, we standardized cone production using the formula:
$CP=CP_i/mean(CP_{sp})$ where *CP*=standardized cone production in a given year, mean(CP_{sp}) =mean number of cones of species *sp* over entire study period, CP_i=number of cones counted in the *i*-th tree of species *sp* in the given year.

In a first step we analysed cone production per species (except for *A. alba* and *P. mugo* for which single-species data series were too short) comparing eight models with a different set of explanatory variables. Four groups of two models were compared: (1) only summer temperature differences ($\Delta T1$) against summer temperatures year $_t$ and year $_{t-1}$; (2) $\Delta T1$ and cone-crop year $_{t-1}$ against summer temperature of year $_t$ and of year $_{t-1}$ and cone-crop year $_{t-1}$; (3) summer temperature differences ($\Delta T2$) against summer temperature of year $_{t-1}$ and of year $_{t-2}$; (4) $\Delta T2$ and cone-crop year $_{t-1}$ against summer temperature of year $_{t-1}$, of year $_{t-2}$ and cone-crop year $_{t-1}$. In a second step, we tested models on the entire dataset (species combined). Also here, we compared models containing the seasonal temperatures and models where we substituted all seasonal temperature with ΔT (Table 3) to test whether the inclusion of ΔT in a more complex model, and not alone as tested by Kelly et al. (2013), could explain greater variance than using seasonal temperatures.
In all cases we used Linear Mixed Effect Models (LMEM) with the standardised average number of cones produced per species and year in a given area as dependent variables and study area as random factor. As cone production was not normally distributed (Shapiro-Wilk's test $W=0.81$: $P < 0.01$) it was ln-transformed. The ln-transformed values met the assumptions of normality (Shapiro-Wilk's test $W=0.95$). The full model contained 14 weather variables and cone production of year $_{t-1}$.
To reduce the number of climate variables, as well as to identify the most significant ones affecting variation in cone production, we performed a stepwise model selection based on AICc (Cavanaugh 1997; Burnham and Anderson 2002) and applied a type III ANOVA to the final model.
Variance in amplitude of the predicted cone production (2015-2099) was further analysed using a general additive model (GAM) with cubic regression splines (Hastie and Tibshirani 1990; Zuur et al. 2009).
All analyses were performed using the R software version 3.1.3 (R Core Team 2015) and packages lme4 (Bates et al. 2014), nlme (Pinheiro et al. 2015), MuMIn (Barton 2014), car (Fox and Weisberg 2011) and mgcv (Wood 2006).

3 Results

Time series of cone production per study area and species did not show clear patterns and, except for two instances, no significant autocorrelation was found (ACF estimates <0.5; Online Resource 1). All species showed marked annual variation in the average number of cones/tree, but clear patterns of masting, followed by a year of poor cone production, were evident in Norway spruce, larch and silver fir (Online resource 2). In species of the genus *Pinus*, annual fluctuations in cone production were less pronounced, although *Pinus cembra* had masting events in the Bormio study area where it was the dominant species (Online resource 2).

3.1 Cone production and climate

Comparison of models proposed by Kelly et al. (2013) with models using the true temperatures are shown in Table 4.

Tabel 4. Linear Mixed Effect Models (LMEMs) with Temperature of summer of year $_t$ (T), Temperature summer of year $_{t-1}$ (T1), Temperature of Summer of year $_{t-2}$ (T2), difference between these Temperatures (ΔT1: T-T1, ΔT2:T1-T2) and ln of cone production of year $_{t-1}$ (cones $_{t-1}$). AICc,weight and significant factors (p<0.05) in bold.

Species	Model	AICc	Weight
Larix decidua	T+T1	66.0	0.351
	ΔT1	64.8	0.649
	T+T1+cones $_{t-1}$	68.8	0.410
	ΔT1+cones $_{t-1}$	68.0	0.590
	T1+T2	65.6	0.425
	ΔT2	65.0	0.575
	T1+T2+cones $_{t-1}$	65.4	0.807
	ΔT2+ cones $_{t-1}$	68.3	0.193
Picea abies	T+T1	87.5	0.253
	ΔT1	85.3	0.747
	T+T1+**cones $_{t-1}$**	80.4	0.219
	ΔT1+**cones $_{t-1}$**	77.9	0.781
	T1+**T2**	81.7	0.398
	ΔT2	80.7	0.602
	T1+**T2**+**cones $_{t-1}$**	76.3	0.270
	ΔT2+ **cones $_{t-1}$**	74.3	0.730
Pinus cembra	T+T1	38.6	0.279
	ΔT1	36.7	0.721
	T+T1+cones $_{t-1}$	43.3	0.274
	ΔT1+cones $_{t-1}$	41.3	0.726
	T1+T2	37.7	0.196
	ΔT2	34.9	0.804
	T1+T2+cones $_{t-1}$	43.1	0.167
	ΔT2+ cones $_{t-1}$	39.9	0.833
Pinus sylvestris	T+T1	33.1	0.007
	ΔT1	23.1	0.993
	T+T1+cones $_{t-1}$	35.1	0.000
	ΔT1+cones $_{t-1}$	57.0	1.000
	T1+T2	32.9	0.008
	ΔT2	23.2	0.992
	T1+T2+cones $_{t-1}$	56.8	0.000
	ΔT2+ cones $_{t-1}$	35.4	1.000
All species	T+T1	193.2	0.192
	ΔT1	190.2	0.818
	T+T1+cones $_{t-1}$	196.9	0.178
	ΔT1+cones $_{t-1}$	193.8	0.822
	T1+**T2**	185.9	0.547
	ΔT2	186.1	0.453
	T1+**T2**+cones $_{t-1}$	189.7	0.531
	ΔT2+ cones $_{t-1}$	190.0	0.469

Significant effects of temperature were found in larch and Norway spruce, the species with the largest datasets. In Norway spruce, and also in *Pinus* species, ΔT performed slightly better than T1+T2 as shown by smaller AICc values and higher model weight (Table 4), but this was not the case for larch. There was little difference between models using ΔT1 or ΔT2, except for Norway spruce and for the models with species combined where models with effects of ΔT2 or temperatures of one and two year before cone production performed significantly better than those using ΔT1 or temperatures of the same summer and of the previous summer. Only in Norway spruce there was a significant and negative effect of the previous year's cone crop on current year's cone production suggesting that resource accumulation and depletion affect cone-crop size. For models with all species there is no difference in the performance between ΔT2 and T1+T2 with ΔAICc < 2.

There was no significant difference between models with and without study area as a random factor (p=0.9), either for models using temperatures or models using ΔT. For models using the temperature difference (ΔT) set of variables, the selected model that best explained annual variation in cone production was:

Lncones = SuDT + SpDT2 + SuP + SuP-1 + WiP + SpP-1

($F_{6,135}$=7.66 ; p<0.01; R^2=0.25).

The selected model that best explained annual variation in cone production using temperatures was:

Lncones = WiT +WiP + SuT-1 + SuP-1 + SuT-2 + SuP-2 + SpT-2

($F_{7,134}$ = 8.62; p<0.01; R^2=0.31; Table 5). The residuals of the selected models did not deviate from a normal distribution (Shapiro-Wilk's test W=0.96).

Table 5. Best model estimates and parameters.

	Estimates	**Std. Error**	**t value**	**p**
Intercept	0.155	0.429	0.360	0.72
WiT	-0.485	0.176	-2.752	<0.01
WiP	1.350	0.540	2.501	0.01
SuT-1	0.725	0.235	3.090	<0.01
SuP-1	0.891	0.296	3.010	<0.01
SuT-2	-0.940	0.288	-3.260	<0.01
SuP-2	-0.894	0.232	-3.849	<0.001
SpT-2	0.804	0.283	2.846	<0.01

Since the model with temperatures (T) performed better than that with ΔT, the following analysis will refer to the model with true temperatures (Table 5). To validate the best model, we calculated a correlation between the observed and predicted estimates of the annual cone crops for the period forest cone production was monitored. Since our weather variables were calculated per macro-area, we averaged annual cone counts within each macro-area, and then combined data for the three macro-areas (n=28). The highly significant correlation (Pearson's r = 0.85; df= 26; p < 0.0001) showed that our model predictions fitted well the actual cone counts (Figure 2).

3.2 Climate projections

Climate projections (2015-2099) display a pronounced temperature increase and a precipitation decrease. The difference in the (non-standardised) average temperature in the period 2090-2099 and that in the period 2015-2024 is 4.45 °C, while the percentage decrease of average precipitation between the same two periods is 25.1 %. Both the temperature increase ($F_{1, 238}$=24.9, p<0.01) and the precipitation decrease ($F_{1, 238}$=23.5, p<0.01) are significant.

Cone production forecast

The best model (Table 5) was then used with climate projection drivers to estimate future cone production in each of the three macro-areas (Online resource 3).

The predicted (ln) cone production did not show any significant trend over time in either of the three macro-areas (AVA $F_{1,85}$=1.46, p=0.22; BAV $F_{1,88}$=0.12, p=0.73; VDA $F_{1,84}$=0.15, p=0.70). This suggests that, even in a scenario with marked temperature increase and significant decrease in precipitation, the predicted warming of the Alps in this century is unlikely to result in either an overall increase or decrease in seed production in conifer forests. Variance of cone production between consecutive years analysed with GAM showed significant differences in macro-area AVA

($F_{6.46}$=3.17, < 0.01; Figure 3). In contrast, there were no significant changes in variance of cone production over time in the other two macro-areas (BAV: $F_{6.27}$=0.69, p = 0.70; VDA: $F_{7.70}$=1.62, p = 0.13; Figure 4). In AVA variance increased gradually, in BAV it seemed to be stable while in VDA predictions suggested increases in the 2030-ties and 2080-ties and a decrease between 2050 and 2075.

4 Discussion

4.1 Weather cues and cone production

There are several climate factors that contribute to masting behaviour of conifer forests across the Alps. Based on our results, summer weather conditions one year and two years before the cones were counted (thus before seed maturation) stand out as the most important variables driving cone production (Kelly et al. 2013). The summer of year t_{-2} corresponds with bud differentiation (into flower or vegetative buds) of spruce, fir and larch, and with bud development in pine species (Farmer 1997; Juday et al. 2003; Roland et al. 2014). During the summer of year t_{-1} spruce, fir and larch flower buds develop while in late spring-early summer the female flowers of pines are pollinated and cone are formed. Apparently, stressful situations (cool, dry summers) promote differentiation into flower buds (negative effects of summer temperature and precipitation on cone production, see Table 5), while warm and wet summers in the year before seed maturation could promote development of flower buds and pollination in pines (positive effects of summer temperature and precipitation on cone production, see Table 5).
Similar effects of temperature have been documented also for other conifers, e.g. Douglas fir and grand fir (Eis 1973) and white spruce (*Picea glauca*) in Alaska (Roland et al. 2014). However, these species responded differently to precipitation patterns: remarkably, the amount of summer precipitation had opposite trends than in this study, which could be related to differences between study sites in total amount and seasonal patterns of precipitation. In effect, a study carried out on white spruce in a different part of its wide distribution range (Southwestern Yukon, Canada) found a negative effect of rainfall during late spring of year t_{-2} (Krebs et al. 2012): hence the opposite than in Alaska for the same species (Roland et al. 2014), but the same as in our multi-species model for the alpine conifers.
Finally, also the conditions in winter had a significant effect: cold and wet winters produce deep snow cover for a long time, which probably enhances water reserves in the soil and thus should reduce water stress to trees in the following spring-summer when conifer seeds mature. In fact, several authors have suggested that conifers in montane and subalpine habitats are sensitive to variations in winter snow-cover and to availability of water in spring-summer (Thomas and Wein 1985; Lévesque et al. 2013)

Where several single-species studies have described relationships between varying weather factors and temporal patterns in tree seed production (e.g. Mencuccini et al. 1995; Pelfini et al. 2006; Casalegno et al. 2010; Crone et al. 2011; Krebs et al. 2012; Walker et al. 2012; Roland et al. 2014), it was not our aim to develop species-specific models relating weather variables to seed production, but to adopt a tree-species community approach. Although this may be considered as a caveat of our study, it must be underlined that the Alps are a heterogeneous environment with many different habitat types occurring at a small scale (few square kilometres), mainly due to the complex mountain orography. This complicates the prediction of ecosystem changes and reactions to perturbations over wide areas. Therefore, we have chosen a "forest type" approach to address and predict spatio-temporal variation in cone production over complex and wide areas such as the montane and subalpine conifer forests of the Alps.
The high correlation between the observed cone counts and those predicted by our model for the period we monitored conifer forest cone production (1999-2013, see Figure 2) suggests our model

is realistic, although considerable variation in cone production remains to be explained. Multi-species studies are relatively rare, but are suggested to help in detecting and predicting general patterns of (changes in) weather factors and how they affect temporal variations in seed production of different plant species distributed over various habitat types (e.g. Broome et al. 2007; Kelly et al. 2013; Wesolowski et al. 2015). Most of these studies have tried to describe and explain the frequency of masting using medium-term (about a decade) to long-term datasets (several decades), but only a few have tried to produce explanatory models using several climate factors. In particular, the work by Kelly et al. (2013) produced multi-species models explaining annual variation in seed-crop size and occurrence of masting events based on the difference in summer temperatures between the year before and 2 years before seed maturation. Also our best model contained summer temperatures (and precipitation, not tested by Kelly et al. 2013) the year before and 2 years before seed maturation and their estimated coefficients had contrasting signs: negative for year t_{-2} and positive for year t_{-1}. Moreover, where we tested the temperature difference (ΔT) model against a model containing the temperatures in years t-2 and t-1 for single species, ΔT performed slightly better for at least some species (e.g. Norway spruce, species with largest dataset). Hence, our models at least partly agreed with Kelly et al. (2013).

4.2 Global warming and future cone production

Conifer seeds are a major food resource for a variety of forest birds and mammals (Boutin et al. 2006; Wauters et al. 2008; Zong et al. 2010, 2012, 2014; Lobo and Millar 2011; Cutini et al. 2013; Dixon and Haffield 2013; Lobo et al. 2013), thus playing an important role in producer-consumer dynamics in the montane and subalpine forest ecosystems. In their review, Koenig and Knops (1998) found inverse relationships between tree-growth and reproduction and their own and a wide range of other studies agree that both processes are correlated with temperature and rainfall. Hence if global warming would affect average amount of seeds produced per year and/or the annual variability in seed production, it could have large effects not just on the forest's primary production and seed production but, through cascade effects, also on the distribution, dynamics and behaviour of a wide range of animal species.

The temperature difference model (Kelly et al. 2013) predicts that masting will be unaffected by increasing mean temperatures under climate change scenarios, but also shows that strongly masting species (such as many of the conifers considered here) should be hypersensitive to climate. However, we know of no study using a medium-term dataset on climate variables and seed (cone) production to develop a model explaining interannual variations in seed production and then using it to estimate future seed crops across different conifer forest types. This work aims at filling this gap.

Using this approach, we found no evidence of long-term changes in the average reproductive investment (seed production) of conifer species and forests in the Alps over 21st century, despite the predicted increase in average temperature and decrease in precipitation. This is in contrast with predictions of increasing seed production due to CO_2 and temperature increase (LaDeau and Clark 2001; but see Hoch et al. 2013 for contrasting results). Hence, where several studies and reviews document and/or predict and increase of tree growth rate, establishment, forest cover and an upward shift of the tree lines in the Alps (e.g. Grace et al. 2002; Vittoz et al. 2008), from our results there are no indications for a substantial change over time in conifer seed production.

As for the amplitude of annual fluctuations in seed production, visual exploration of the predicted cone crops suggests that in all three macro-areas, thus in all the different conifer forest types that were monitored, large variation between seed-crop failures and mast crops is maintained. However, in one macro-area, AVA, our GAM model suggests a significant increase in the amplitude of fluctuations in cone-crop size over time. The AVA study area has lower predicted cone production than the others sites (forests with an important component of *Pinus* sp., that produce on average fewer cones than spruce or larch). Interestingly, predicted seasonal precipitation in AVA varies less strongly than in the other two macro-areas (BAV and VDA). These differences between areas in variation in seasonal precipitation could result in spatial variation in events of drought stress, that can reduce tree growth, increase tree mortality (Guarin and Taylor 2005; Allen et al. 2010; Williams et al. 2013) and potentially affect reproductive investment. The predictive models used here suggest that there will be little or no change in the current pattern of annual fluctuations in cone production, where a mast year is followed by one or two years of poor-medium cone production or even cone failure, in agreement with the temperature difference model (Kelly et al. 2013).

Finally, it must be emphasised that this is a first set of predictive models investigating the effects of a global warming scenario on conifer cone production in montane and subalpine forest ecosystems in the Alps, and that several environmental factors that are potentially important for plant reproduction, such as changes in wind, soil moisture and nutrient limitation (e.g. Callahan et al. 2008; Hoch et al. 2013), have not been included.

5 Conclusions

Four out of six conifer species in our study areas in the Italian Alps showed clear patterns of masting, with intermittent years of poor seed production. The occurrence of extremely large seed-crops, and/or seed-crop failures, was less pronounced in two pine species, *Pinus sylvestris* and *P. mugo*. For *P. sylvestris* a reduced amplitude of seed-crop fluctuations has been reported also in other parts of its range (e.g. Wauters et al. 2001, 2004), while we found no literature data on long-term trends in *P. mugo* seed production. Weather factors in summer, both temperature and precipitation one and two years prior to seed maturation, were most strongly correlated with annual fluctuations in cone-crop size. Our estimates of trends in future cone production, under a global warming scenario of higher temperatures and reduced precipitation over the next 85 years, suggest that conifer species in the Alps will continue to produce fluctuating cone crops without a significant increase or decrease in average cone production. Nevertheless, future scenarios suggest spatial variation in trends of cone production with increasing episodes of large cone-crops at some time in the future in two macro-areas, that could affect ecosystem equilibrium. Future variation in conifer masting and synchrony could affect seed predators population dynamics, as for example reported by Archibald et al. (2012) who analysed white spruce (*Picea glauca*) intra-annual reproductive synchrony. They found that trees with cones that mature synchronously are more likely to escape predation by a specialist seed predator (North-American red squirrel, *Tamiasciurus hudsonicus*), generating positive selection and thus increasing intra-annual reproductive synchrony. We can therefore hypothesize that, even if future global warming will not directly affect single species dynamics, as conifer reproductive strategies, small changes could dephase the delicate squirrel-conifer equilibrium. To explore this hypothesis, both long-term time-series of conifer seed production and demography of squirrels (seed consumer) (e.g. Boutin et al. 2006; Wauters et al. 2008; Williams et al. 2014), as well as models testing combined effects of future global warming scenarios and the resulting trends in future cone crops on the consumer dynamics, are necessary.

Conflict of Interest: The authors declare that they have no conflict of interest.

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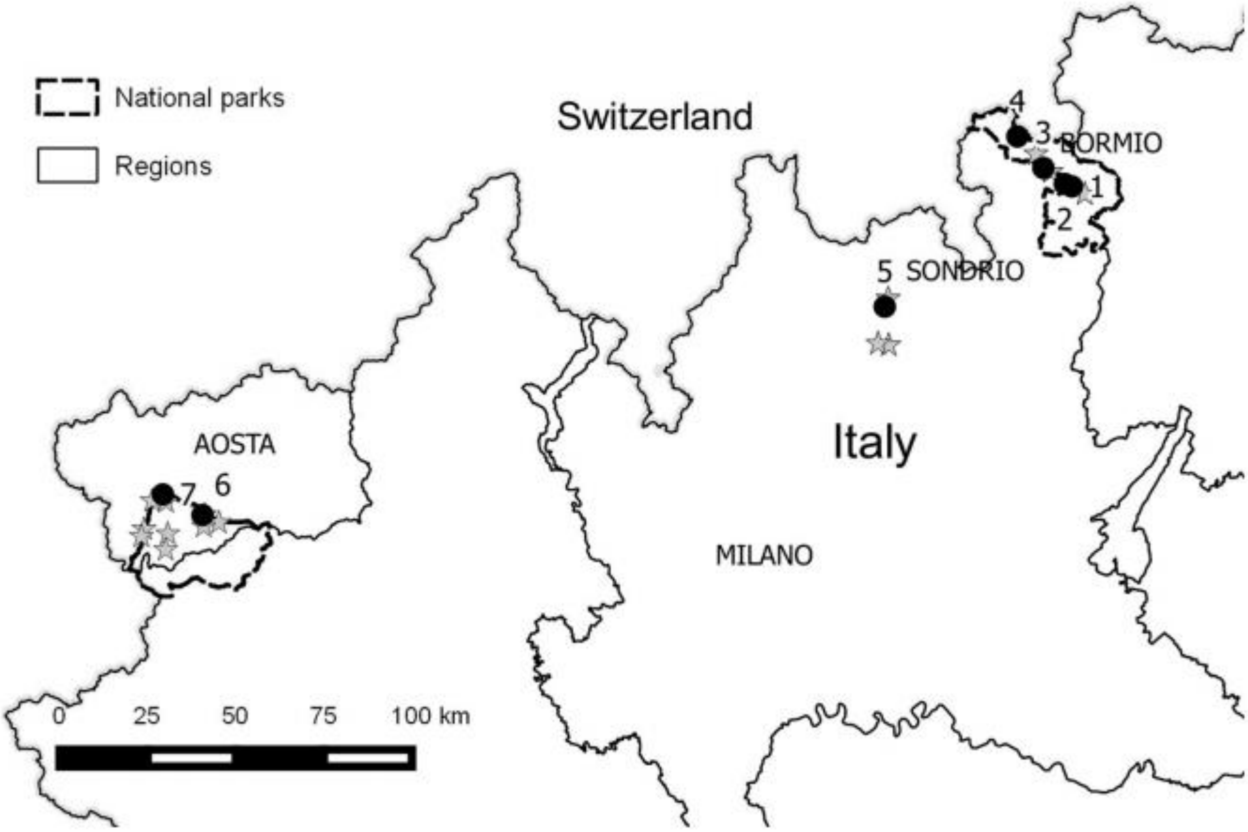

Fig. 1 Study area. Black dots correspond to study sites: 1. Valfurva (VAL), 2 Bormio (BOR), 3 Oga (OGA), 4 Cancano (CAN), 5 Cedrasco (CED). 6 Cogne (COG), 7 Rhemes (RHE). Grey stars represent meteorological stations

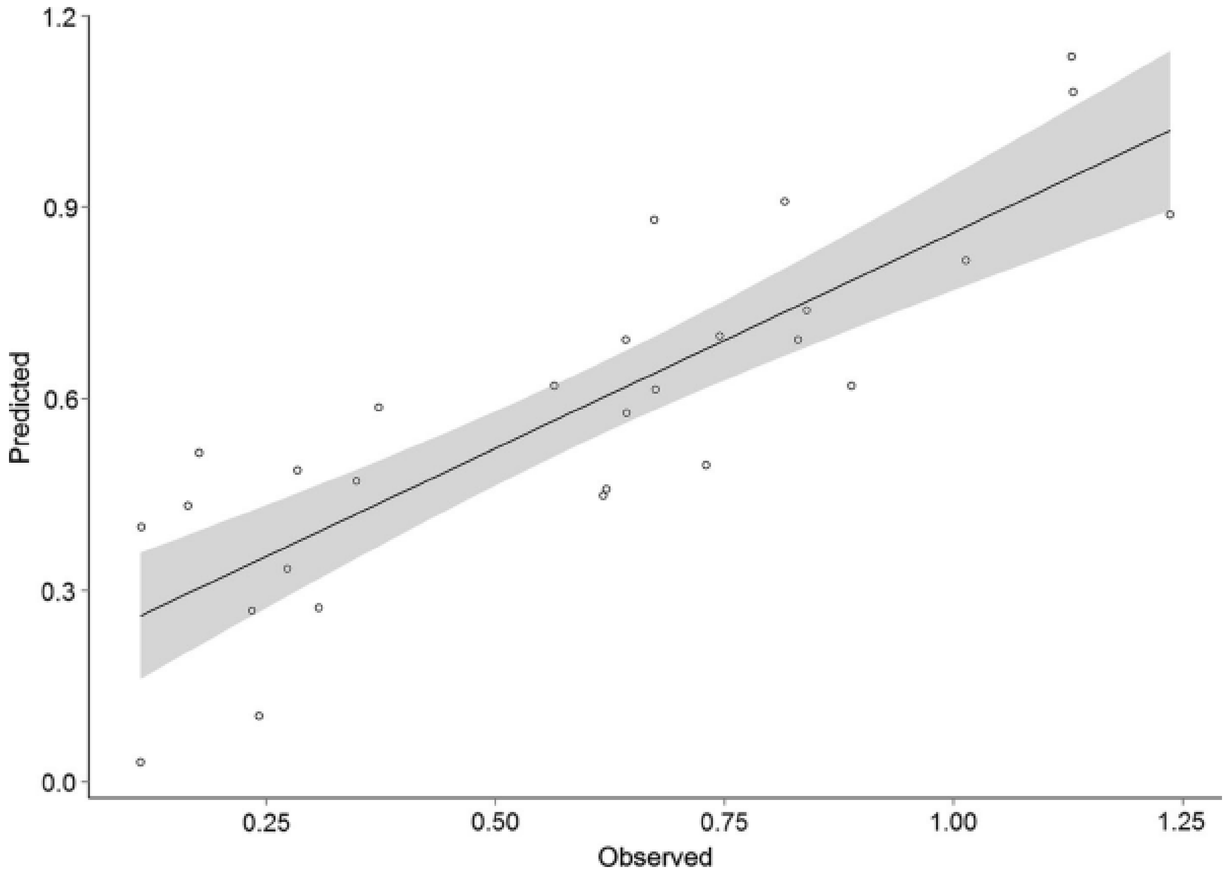

Fig. 2 Observed and predicted annual conifer cone crops averaged per macro-area. Predicted counts are from the best model parameter estimates (see table 4)

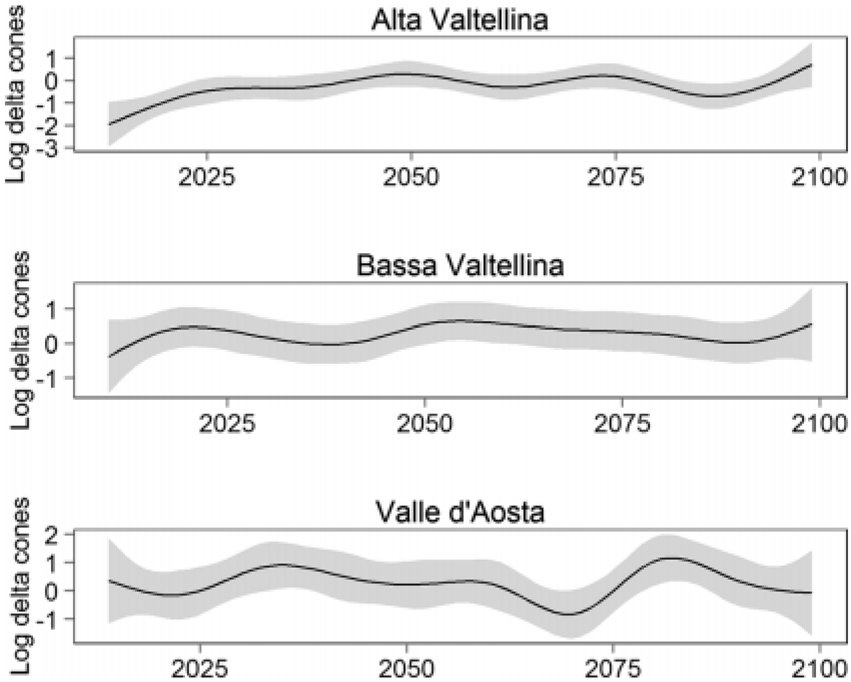

Fig. 3 GAM of variance of cone production. Smoothing factor: Alta Valtellina 8, Bassa Valtellina 12, Valle d'Aosta 10

Online Resource 1 Autocorrelation Function estimates, in bold significant correlation
Online Resource 2 Seed production for each area and species
Online Resource 3 Cones prediction