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Electronic supplementary material

ESM 1
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ESM 2
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ESM 3
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An improved species distribution model for Scots pine and downy oak under future climate change in the NW Italian Alps

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10 Received: 16 March 2014 / Accepted: 10 November 2014
11 © INRA and Springer-Verlag France 2014**Abstract**

• **Context** Scots pine is currently declining in most inner alpine sectors of southern Europe. The relative contribution of climate, land use change, and disturbances on the decline is poorly understood. What will be the future distribution of the species? Is vegetation shifting toward oak-dominated forests? What is the role of extreme drought years?

• **Aims** The aims of the study were to determine drivers of current distribution of Scots pine and downy oak in Aosta valley (SW Alps), to extrapolate species distribution models to year 2080 (Special Report on Emissions Scenarios (SRES) A1B), and to assess the ability of pine vitality response to the extreme droughts in 2003 and 2006 to predict modeled vegetation changes.

• **Methods** Ensemble distribution models were created using climate, topography, soil, competition, natural disturbances, and land use. Species presence was derived from a regional forest inventory. Pine response to drought of 2003–2006 was assessed by Normalized Difference Vegetation Index (NDVI) differencing and correlated to modeled cover change between 2080 and present.

• **Results** Scots pine and downy oak were more likely to occur under higher climatic aridity. Scots pine was also associated to higher wildfire frequency, land use intensity, and lack of

competition. In a warming scenario, pine experienced an elevational displacement. This was partially counteracted if no land abandonment was hypothesized. Downy oak cover increased in all scenarios. Short- and long-term drought responses of pine were unrelated.

• **Conclusion** Warming will induce an upward displacement of pine, but this can be partially mitigated by maintaining a more intense land use. The drought-induced decline in pine vitality after extreme years did not overlap to the modeled species response under climate warming; responses to short-term drought must be more thoroughly understood in order to predict community shifts.

Keywords Drought · Pine decline · *Pinus sylvestris* L. · Potential niche · *Quercus pubescens* Willd · Succession

1 Introduction

Scots pine (*Pinus sylvestris* L.) forests at the southern edge of their distribution are currently facing decline and succession, resulting from a combination of climate warming, land use changes, and increased abiotic and biotic disturbances (Gimmi et al. 2010; Vacchiano et al. 2012).

From a physiological standpoint, drought has been identified as the primary driver of pine decline, as it affects foliage production, carbon allocation (Galiano et al. 2010), cambial activity (Eilmann et al. 2011; Oberhuber et al. 2011), hydraulic capacity (Sterck et al. 2008), and the likelihood of xylem cavitation (Martínez-Vilalta and Piñol 2002). Additionally, drought can predispose weakened trees to inciting mortality agents, such as mistletoe, bark beetles, or root-rot fungi (Dobbertin et al. 2007; Gonthier et al. 2010; Rigling et al. 2010; Sangüesa-Barreda et al. 2013).

On top of this, at the landscape level, Scots pine forests in southern Europe have recently experienced a decrease in

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68 management intensity, shifting from open-canopy, even-aged
 69 stands maintained by broadleaves coppicing, wood pasture,
 70 litter raking, and pitch collection (Gimmi et al. 2007) to denser
 71 forests following depopulation of mountain areas and aban-
 72 donment of traditional land use practices. Under such scenar-
 73 io, succession by mid-tolerant species such as downy oak
 74 (*Quercus pubescens* Willd.) is favored over Scots pine regen-
 75 eration (Urbíeta et al. 2011; Rigling et al. 2013). Both mech-
 76 anisms, land use changes and climate extremes, are at work at
 77 the same time (Gimmi et al. 2010), determining feedbacks and
 78 interactions difficult to disentangle and providing a challenge
 79 for forecasting future vegetation patterns.

80 Recessions of Scots pine forests in southern European land-
 81 scapes would affect the provision of important ecosystem
 82 services, such as protection from hydrogeological hazards,
 83 plant and animal diversity, timber, and recreation. A shift from
 84 Scots pine to oak can also be problematic because of the loss
 85 of useful life traits, as the ability to rapidly colonize open or
 86 disturbed ground (Vacchiano et al. 2013). Predictions of future
 87 vegetation changes and knowledge of the suitability of pine
 88 vs. oak to expected environmental conditions will help man-
 89 agers in developing adaptation strategies to sustain the fulfill-
 90 ment of the desired forest functions (Chmura et al. 2011).

91 The aims of this work were (1) to detect drivers of current
 92 pine and oak occurrence in a mountain region of the south-
 93 western Alps, by fitting species distribution models (SDM) on
 94 climate, soil, anthropogenic stand structure, and disturbance-
 95 related predictors; (2) to apply the models using future (2080)
 96 scenarios, in order to assess if and where vegetation shifts are
 97 likely to occur under climate and management changes; and
 98 (3) to compare the effects of the Europe-wide drought events
 99 of 2003 and 2006 (Thabeet et al. 2010) on Scots pine vitality
 100 against SDM predictions in 2080, in order to assess the
 101 potential role of extreme drought response as an early warning
 102 of future vegetation changes.

103 2 Methods

104 2.1 Study species

105 Scots pine is the most widespread coniferous species in Eu-
 106 rope and the most widespread pine in the world (Mirov 1967).
 107 Scots pine is a species of continental climates, able to grow in
 108 areas with annual precipitation ranging from 200 to 1800 mm
 109 (Burns and Honkala 1990). The upper/northern and lower/
 110 southern limits of the species correspond with isotherms
 111 -1°C (mean temperature of the coldest month) and $+33^{\circ}\text{C}$
 112 (mean temperature of the warmest month), respectively (Dahl
 113 1998), even if pine can tolerate more extreme temperatures
 114 without tissue damage, especially at the cold end (-90°C :
 115 Sakai and Okada 1971).

116 Scots pine is a light-demanding, early seral species that can
 117 establish both in acid and limestone soils (Richardson 1998;
 118 Debain et al. 2003). Its ecology is largely characterized by
 119 stress tolerance. On the one hand, this allows it to occupy a
 120 range of habitats that are unfavorable to other tree species,
 121 through tolerating various combinations of climatic and
 122 edaphic stress (Richardson 1998). On the other hand, this
 123 implies that Scots pine is excluded from more favorable sites
 124 through competition. In recent decades, it was favored by past
 125 fires (Gobet et al. 2003), by heavy forest cuts, and by the
 126 recent increase of fallow lands (Farrell et al. 2000; Kräuchi
 127 et al. 2000; Caplat et al. 2006; Picon-Cochard et al. 2006). In
 128 the absence of disturbances, it will eventually be overgrown or
 129 replaced by broadleaves or mixed broad-leaved coniferous
 130 forest. However, in the drier, central alpine sectors
 131 ($<700 \text{ mm year}^{-1}$ rainfall), Scots pine often forms stable
 132 communities due to limited competitiveness of other conifer
 133 tree species (Ozenda 1985).

134 Scots pine populations are negatively affected by drought
 135 in all demographic processes, i.e., regeneration (Carnicer et al.
 136 2014, Galiano et al. 2013), growth (Vilà-Cabrera et al. 2011),
 137 and mortality (Dobbertin et al. 2005; Bigler et al. 2006). On
 138 the other hand, downy oak exhibits better ecophysiological
 139 adaptations (Nardini and Pitt 1999; Eilmann et al. 2006, 2009;
 140 Zweifel et al. 2009) and higher growth (Weber et al. 2008)
 141 under comparable climate conditions. Oaks also have an
 142 advantage over Scots pine in the regeneration phase following
 143 stand-replacing fire, owing to their resprouting ability—as
 144 opposed to limitations in Scots pine regeneration due to short
 145 dispersal distance and obligate seeder traits (Moser et al. 2010;
 146 Vacchiano et al. 2013). Such differences, and the fact that oaks
 147 are characterized by lower shade intolerance, make them a
 148 suitable species for secondary succession of declining or
 149 outcompeted pine stands.

150 2.2 Study area

151 The study area covers the Aosta Valley region in Northwestern
 152 Italy (3262 km^2) (Fig. 1). Topography is shaped by a main
 153 east–west-oriented valley with several north–south protrusions.
 154 Mean annual temperature in Aosta ($45^{\circ} 26' \text{ N}, 7^{\circ} 11' \text{ E}$,
 155Q8 583 m a.s.l.) is 10.9°C (years 1961–1990; Tetrarca et al.
 156 1999). Climate is warm-summer continental (Dfb) according
 157 to the Köppen classification (Peel et al. 2007); July and
 158 January monthly means may differ by as much as 22°C . Mean
 159 annual rainfall in Aosta amounts to very low values in com-
 160 parison with localities in other central Alpine valleys
 161 (494 mm, years 1961–1990; Biancotti et al. 1998), with a
 162 period of water deficit (Bagnouls and Gaussen 1957) extend-
 163 ing from June to September. Winter precipitation usually
 164 comes as snow. The study area exhibits both crystalline
 165 (granites) and metamorphic bedrocks, but most landscape is
 166 covered by quaternary deposits of glacial, gravitational, or

167 colluvial origin. Soils belong to the series of western and
 168 central Alpine soil on igneous and metamorphic rocks
 169 (Costantini et al. 2004) and are mostly represented by shallow
 170 soils (Lithic, Umbric, and Dystric Leptosols), eroded soils
 171 (Eutric and Calcaric Regosols), acid soils with organic matter,
 172 iron oxides and aluminum accumulation (Dystric Cambisols,
 173 Haplic Podzols, Humic Umbrisols), or alluvial soils (Eutric
 174 Fluvisols).

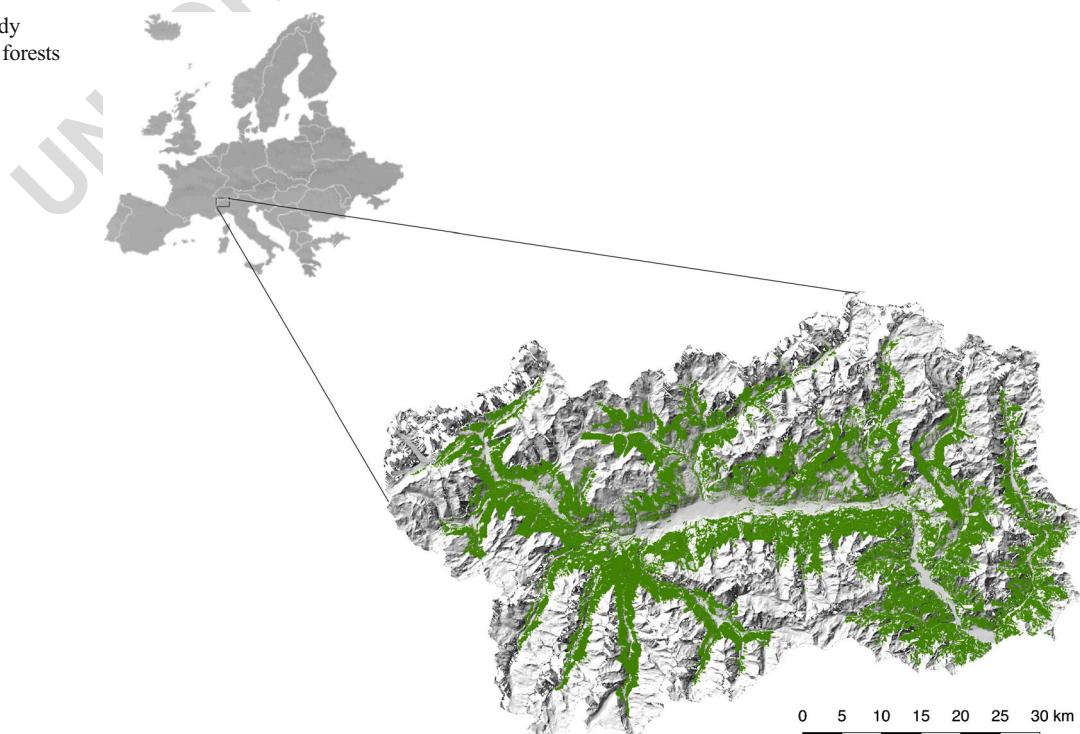
175 Scots pine stands in the study area cover 5372 ha
 176 (Gasparini and Tabacchi 2011), i.e., 6 % of the total forest
 177 area, and thrive on both acidic and basic substrates of well-
 178 exposed, bottom to mid-elevation slopes. Stands dominated
 179 by Scots pine are mostly young, averaging 920 trees per
 180 hectare (TPHA) and a basal area (BA) of 26 m² ha⁻¹
 181 (Gasparini and Tabacchi 2011). Quadratic mean diameter
 182 (QMD) is 21 cm, but trees larger than 35 cm are extremely
 183 rare (about 2 %) (Camerano et al. 2007). Stand top height can
 184 vary from 10 to 25 m according to site fertility (Vacchiano
 185 et al. 2008). Depending on successional stage and climatic
 186 factors, species composition may range from 100 % pine
 187 (especially on recently disturbed sites or dry, southern slopes)
 188 to mixtures with Swiss mountain pine (*Pinus montana* Mill.),
 189 European larch (*Larix decidua* Mill.), Norway spruce (*Picea
 190 excelsa* Karst.), silver fir (*Abies alba* Mill.), beech (*Fagus
 191 sylvatica* L.), sessile oak (*Quercus petraea* (Mattus.) Liebl.),
 192 European chestnut (*Castanea sativa* Mill.), and mostly with
 193 downy oak, which has similar thermal and moisture needs.

194 Downy oak stands cover 3468 ha in the study area
 195 (Gasparini and Tabacchi 2011), at elevations of 300–1200 m
 196 (but up to 1500 m on rocky outcrops and 1800 m for isolated
 197 individuals), predominantly on shallow soils and carbonatic
 198 substrates. Xerophilous stands on south-facing slopes are
 199 sparse and slow growing (1000 TPHA, BA 20 m² ha⁻¹), with
 200 young individuals often developed from former coppices,
 201 grazed woodland, or after invasion on abandoned fallow lands
 202 (QMD 10–25 cm, mean height 5–10 m) (Gasparini and
 203 Tabacchi 2011). Just as in Scots pine, meso-xerophilous
 204 stands on north-facing slopes exhibited higher growth (mean
 205 height 10–15 m) and a mixture degree. Scots pine and downy
 206 oak can replace each other in the course of forest dynamics,
 207 e.g., by regeneration of pine in sparse and degraded oak
 208 woodlands or the succession of closed-canopy, or declining,
 209 pine forests to more tolerant oak (Zavala and Zea 2004).

2.3 Drivers of pine and oak distribution

In order to model the occurrence of Scots pine and downy oak
 in the study area, we used a diverse set of explanatory variables
 including vectorial as well as raster information at different
 spatial resolutions. All variables were resampled at a common
 spatial resolution of 1 km, i.e., the coarsest resolution
 among all explanatory variables, and clipped to a land use
 mask of current forest distribution. In fact, we decided to
 exclusively include presence/absence of pine and oak in areas
 211
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 217Q9
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Fig. 1 Location of the study region and area covered by forests (in green)



219 with forest cover, since the model could be calibrated against
 220 current vegetation conditions only. Rasterization of vector
 221 layers and raster resampling were carried out by aggregating
 222 to cell means if raster grain was finer than 1 km and by bilinear
 223 (for continuous layers) or nearest neighbor interpolation (for
 224 categorical layers) if grain exceeded 1 km (Figure S1). Ex-
 225 planatory variables included the following:

- 226 (1) Elevation, slope, aspect, southness (i.e., a linearization of
 227 aspect: Chang et al. 2004), and topographic position
 228 index (TPI: Guisan et al. 1999) computed from a 10-m
 229 digital terrain model. A higher TPI is indicative of ridges
 230 or hilltops.
- 231 (2) Climate means (years 1961–1990) at a 1-km resolution,
 232 extracted from the WorldClim database (Hijmans et al.
 233 2005). These included mean, minimum, and maximum
 234 yearly temperatures (TMIN, TMEAN, TMAX), yearly
 235 precipitation (P), precipitation cumulated in the growing
 236 season (GSP; April–September), and yearly solar radia-
 237 tion (RAD). Additionally, using mean, minimum, and
 238 maximum monthly temperature grids, we computed
 239 growing degree days (GDD; base temperature=5 °C)
 240 (Fronzek et al. 2011) and an aridity index (AI) as the
 241 difference between monthly precipitation and potential
 242 evapotranspiration (PET). PET for month i was comput-
 243 ed as after Zimmermann et al. (2007).

$$\text{RAD}_i(T\text{MEAN}_i + 17.8) \frac{(T\text{MAX}_i - T\text{MIN}_i)}{2} \text{ days}$$

244

- 245 (3) Soil variables at a 1-km resolution, extracted from the
 246 European Soil database (European Soil 1999). We se-
 247 lected variables potentially important for tree establish-
 248 ment and growth, namely available water capacity
 249 (AWC) of the topsoil, accumulated soil temperature class
 250 (ATC), total organic carbon (OC) of the topsoil, base
 251 saturation (BS), erodibility (ERO), depth to rock (DR),
 252 dominant surface textural class (TEXT), and volume of
 253 stones (VS). All variables were coded as dummy values.
- 254 (4) Natural disturbances, such as landslides or severe soil
 255 erosion (source: Corine Land Cover 1990 raster cover-
 256 age, resolution 500 m), avalanche tracks, and wildfires
 257 >10 ha for the years 1961–1991 (sources: Regione
 258 Autonoma Valle d'Aosta, Ufficio Neve e Valanghe, and
 259 Regione Autonoma Valle d'Aosta, Corpo Forestale
 260 Regionale, Nucleo Antincendo Boschivi).
- 261 (5) Competition by the pre-existing canopy, assessed by
 262 extracting the Normalized Difference Vegetation Index
 263 (NDVI) from a Landsat 5 Thematic Mapper image (path
 264 195, row 28) taken on June 30, 1987 (resolution 30 m).
 265 The acquisition period was chosen as to be at the peak at
 266 the growing season; the image had 10 % cloud cover, but

267 clouds were clustered over high elevation, unforested
 268 terrain. The image was first converted to top of the
 269 atmosphere radiance using standard equations and cali-
 270 bration parameters obtained from the metadata of each
 271 scene (Chander et al. 2009). Then, we computed NDVI
 272 using band TM4 (near infrared) and band TM3 (visible
 273 red) and used it as a proxy of standing forest biomass
 274 (Tucker 1979; Pettorelli et al. 2005). As an additional
 275 index of competition by forest vegetation, we used per-
 276 cent tree cover from the recently released Landsat vege-
 277 tation continuous field (VCF) dataset (Sexton et al.
 278 2013), at a resolution of 30 m, based on a Landsat 5
 279 TM image acquired on July 27, 2001.

- 280 (6) Land use intensity was assessed by using proxy variables,
 281 i.e., total road length and total building surface per 500-m
 282 pixel, as extracted from a vector regional map. Moreover,
 283 the degree of land abandonment was estimated at the
 284 municipality level by the percent variation in resident
 285 population in the period 1951–1991 (source: ISTAT).

286 In order to limit collinearity of independent variables,
 287 predictors exhibiting a Pearson's correlation coefficient
 288 >|0.9| were excluded from further analysis.

290 2.4 Model runs under future scenarios

291 Simulation experiments for the future projections of species
 292 distribution relied on the same set of explanatory variables.
 293 However, values for variables used in future scenarios were
 294 chosen as follows:

- 295 (1) Climate means for the 2080 decade were extracted from
 296 30-arcsec gridded simulations by the ECHAM5/MPI-
 297 OM model from the Max-Planck Institute for Meteorol-
 298 ogy, Germany (Raible et al. 2006), under the high emis-
 299 sion scenario Special Report on Emissions Scenarios
 300 (SRES) A1B. Under the assumption of a constant solar
 301 radiation, we computed GDD, GSP, PET, and AI from
 302 the ECHAM-5 grids. For the 2080 scenario, we did not
 303 extrapolate the model to pixels exhibiting AI values
 304 exceeding the range of current ones (Elith and Leathwick
 305 2009).
- 306 (2) Fire frequency and size are supposedly responsive to
 307 climate change (Moriondo et al. 2006). In order to sim-
 308 ulate the influence of fire preceding the 2080 decade, we
 309 used wildfire polygons for the years 1981–2000, i.e., a
 310 period that included several extreme fire seasons
 311 resulting in a +39 and +26 % increase in the frequency
 312 and total area burned, respectively, by large fires (>10 ha)
 313 relative to 1961–1980.
- 314 (3) We simulated two alternative land use scenarios: (1)
 315 urbanization and land abandonment, i.e., every munici-
 316 pality was assigned a “business as usual” scenario of

317 population change using figures for the period 1951–
 318 1991 and (2) maintenance of high land use, i.e., all
 319 municipalities were assigned 0 % variation in population
 320 respective to 1951, thereby assuming a continued pres-
 321 ence of man and its activities at all rural settings.

322 Soil characteristics are also responsive to climate change
 323 (Singh et al. 2011); however, we kept these variables at current
 324 conditions for the 2080 simulation, since no quantitative sce-
 325 narios are available to estimate future changes. Altogether,
 326 three scenarios were simulated: current conditions, 2080 cli-
 327 mate with unchanged land use, and 2080 climate with intense
 328 land use.

329 2.5 Model building

330 Presence/absence of pine and oak in the years 1992–1994
 331 served as a response variable, which we extracted from a
 332 regional forest inventory based on a 500-m regular grid. At
 333 every grid node, the species and diameter at breast height
 334 (DBH) of each living tree (DBH >7.5 cm) were measured
 335 within a variable-radius circular plot (radius 8–15 m depend-
 336 ing on tree density). Plot coordinates were recorded to the
 337 nearest meter. Scots pine and downy oak were labeled as
 338 present where at least one tree of each species was recorded
 339 and absent otherwise.

340 We assumed that both pine and oak distribution are in
 341 equilibrium with the environment (Rohde 2005). For this
 342 reason, and because our aim was to model potential niche,
 343 no migration constraints were included in the model.

344 We used an ensemble modeling approach (Araujo and New
 345 2007), by fitting and averaging predictions obtained by a
 346 generalized linear model (GLM), artificial neural network
 347 (ANN), and multiple adaptive regression spline (MARS)
 348 using the same set of responses, predictors, and scenarios.
 349 Model specifications were as follows: (a) for GLM, a back-
 350 ward stepwise algorithm was used, based on Akaike Informa-
 351 tion Criterion (AIC); (b) for ANN, the initial number of cross-
 352 validations to find best size and decay parameters was set to
 353 five; and (c) for MARS, the cost per degree of freedom charge
 354 was set to 2, and the model was pruned in a backward stepwise
 355 fashion. All models were fit on a binomial distribution with
 356 logit link, without interactions between predictors, and using a
 357 maximum of 100 iterations.

358 For each of the three models, we computed variable impor-
 359 tance ratings and response curves. To do so, all variables but
 360 one are set constant to their median value, and only the remain-
 361 ing one is allowed to vary across its whole range. In the case of
 362 categorical variables (e.g., soil), the most represented class was
 363 used. The variations observed and the curve thus obtained show
 364 the sensibility of the model to that specific variable.

365 We carried out k -fold cross-validation of the model by
 366 subdividing the data into a 3:1 proportion ($k=4$). Model

367 specificity and sensitivity were computed for the selected
 368 thresholds; the threshold to convert continuous predictions
 369 into binary ones was iteratively chosen to maximize the area
 370 under the curve (AUC).

371 The ensemble prediction was computed from all model
 372 realizations with AUC >0.75. The probability of occurrence
 373 for the ensemble prediction was the mean of the selected
 374 models' predictions, weighted by the model AUC. Model
 375 residuals were scrutinized to detect the absence of trends
 376 against predicted values and independent variables; a
 377 variogram was fitted to assess the degree of residual spatial
 378 autocorrelation. Ensemble models were run for the whole
 379 study region to obtain a map of potential species distribution
 380 under current and future climate, assuming niche
 381 conservatism (Wiens et al. 2010). We classified simulated
 382 presence/absence of both species using an occurrence proba-
 383 bility threshold of 0.6 and assessed projected area changes and
 384 elevational shifts in the distribution of pine and oak under the
 385 climate change and climate change intense land use scenarios.
 386 All analyses were carried out using the biomod2 package
 387 (Thuiller et al. 2013) for R (R Development Core Team 2013).

388 2.6 Effect of extreme drought events

389 The response of extant Scots pine forests to drought events in
 390 years 2003 and 2006 was assessed by the temporal difference
 391 in NDVI (Δ NDVI: year of drought – year before drought).
 392 NDVI was computed from two 16-day maximum value com-
 393 posite (MVC) MODIS images (resolution 30 arcsec) taken at
 394 the end of the summer (Julian days 226–241). Cloud cover of
 395 the MVC was between 1 and 4 % for the four images. Pixels
 396 with a quality analysis score of 2 and 3 (i.e., targets covered by
 397 snow/ice or cloudy pixel) as well as NDVI lower than 0.2 or
 398 null (open water) were filtered out (Vacchiano et al. 2012).

399 In order to distinguish reflectance anomalies from random
 400 or systematic error (Morisette and Khorram 2000), we classi-
 401 fied as “decline” all pixels with Δ NDVI < (mean – 3 standard
 402 deviations), as computed from the full scene (Fung and
 403 LeDrew 1988; Vacchiano et al. 2012). Finally, we compared
 404 the modeled change in pine occurrence probability (2080–
 405 current) of decline vs. non-decline pixels by means of
 406 Wilcoxon signed-rank test (Sokal and Rohlf 1995).

408 3 Results

409 Scots pines were detected in 460 (27 %) out of 1730 inventory
 410 plots, and downy oak in 181 (10 %). After screening for
 411 collinearity, 18 predictors were retained for subsequent anal-
 412 yses (Table 1). Since most climate-related variables were
 413 correlated to each other and to elevation, we retained only
 414 aridity index (AI) as the main climate predictor; Pearson's

Q12 t1.1 **Table 1** Explanatory variables used in this study (minimum, maximum, mean, standard error), computed for currently forested areas only

t1.2	Code	Description	Range	Mean	Units	Resolution
t1.3	Bio01	Mean annual temperature ^a	-0.6–11.1	4.9	°C	30 arcsec
t1.4	Bio05	Max temperature of warmest month ^a	10.8–26.7	18.5	°C	30 arcsec
t1.5	Bio06	Min temperature of coldest month ^a	-10.8–2.9	-6.9	°C	30 arcsec
t1.6	Bio07	Temperature annual range ^a	21.3–29.6	25.4	°C	30 arcsec
t1.7	Bio10	Mean temperature of warmest quarter ^a	6.4–20	12.8	°C	30 arcsec
t1.8	Bio11	Mean temperature of coldest quarter ^a	-7.2–2	-2.8	°C	30 arcsec
t1.9	Bio12	Annual precipitation ^a	796–1828	1263.3	mm	30 arcsec
t1.10	Bio18	Precipitation of warmest quarter ^a	22–465	335.6	mm	30 arcsec
t1.11	GDD	Growing degree days above 5 °C	257–2656	1181.2	°C	30 arcsec
t1.12	GSP	Precipitation April–September	437–913	663.5	mm	30 arcsec
t1.13	AI	Aridity index (bio12 -PET)	-638–1252	311.0	mm	30 arcsec
t1.14	DTM	Elevation ^b	308–2493	1514.3	m a.s.l.	10 m
t1.15	Slope	Slope from DTM	0–44	17.0	°	10 m
t1.16	TPI	Topographic position Index	-3.0–3.1	-0.4	—	10 m
t1.17	Southness	Linearization of aspect	0–180	97.2	°	10 m
t1.18	ATC	Accumulated Soil temperature class ^c	1–3	—	Dummy	1 km
t1.19	AWC	Available water capacity in the topsoil ^c	1–3	—	Dummy	1 km
t1.20	BS	Soil base saturation ^c	1–2	—	Dummy	1 km
t1.21	DR	Soil depth to rock ^c	1–4	—	Dummy	1 km
t1.22	ERO	Soil erodibility ^c	3–5	—	Dummy	1 km
t1.23	OC	Organic carbon in the topsoil ^c	1–3	—	Dummy	1 km
t1.24	TEXT	Soil texture (from coarse to fine) ^c	0–2	—	Dummy	1 km
t1.25	VS	Volume of stones in the soil ^c	0–2	—	Dummy	1 km
t1.26	Avalanches	Number of avalanche polygons ^b	0–3	0.1	Count	10 m
t1.27	Wildfires	Number of fire polygons, 1961–1990 ^b	0–3	0.0	Count	10 m
t1.28	Erosion	Total area subject to landslide or erosion ^d	0–14,523	656.9	m ²	500 m
t1.29	Depop	Change in population 1951–1991 ^e	-59–135	2.1	% change	Municipality
t1.30	Roads	Total road length ^b	0–8485	1812.0	m	500 m
t1.31	Buildings	Total buildings area ^b	0–40,190	1591.8	m ²	500 m
t1.32	VCF	Tree cover from Landsat (2001) ^f	0–99	29.9	%	30 m
t1.33	NDVI	NDVI from Landsat (1987)	0.20–0.66	0.30	0–1	30 m

Explanatory variables in species distribution models are set in italics

^aHijmans et al. (2005)

^bRegione Autonoma Valle d'Aosta

^cEuropean Soil (1999)

^dEuropean Environment (2013)

^eISTAT (2012)

^fSexton et al. (2013)

415 correlation between AI and WorldClim variables was always
416 higher than 0.95 (e.g., $R=-0.995$ vs. mean annual temperature,
417 $R=0.993$ vs. annual precipitation, $R=-0.962$ vs. GDD).

418 AI was the most important predictor for the current distribution
419 of both pine and oak (Table 2), with higher occurrence
420 probability at low water balance levels (Figure S2). However,
421 MARS captured a reduced probability of occurrence for Scots

422 pine at very low values of the aridity index (i.e., very dry
423 sites). Beyond aridity, variables associated to high probability
424 of Scots pine occurrence were southness, TPI, population
425 change, building density, and past fires—the last two only in
426 the ANN model. Soil erosion, NDVI, and road density (in the
427 ANN model) decreased the probability of pine presence
428 (Figure S2a). Explanatory variables of oak distribution

t2.1 **Table 2** Variable importance (0–1) for SDM of current Scots pine and
downy oak distribution fitted by generalized linear model (GLM),
artificial neural network (ANN), and multiple adaptive regression spline
(MARS)

t2.2		Scots pine			Downy oak			
		GLM	MARS	ANN	GLM	MARS	ANN	
t2.4	AI	0.650	0.645	0.733	0.848	0.830	1.000	453
t2.5	Slope	0.000	0.086	0.006	0.038	0.087	0.023	454
t2.6	TPI	0.145	0.162	0.000	0.099	0.103	0.000	455
t2.7	Southness	0.180	0.393	0.283	0.210	0.269	0.220	456
t2.8	ATC	0.000	0.017	0.000	0.078	0.042	0.000	457
t2.9	AWC	0.000	0.000	0.000	0.000	0.000	0.000	458
t2.10	DR	0.000	0.000	0.000	0.251	0.138	0.000	459
t2.11	ERO	0.000	0.000	0.000	0.000	0.000	0.000	
t2.12	OC	0.000	0.000	0.000	0.044	0.000	0.000	
t2.13	VS	0.000	0.000	0.000	0.160	0.000	0.000	
t2.14	Avalanches	0.000	0.000	0.000	0.000	0.000	0.000	
t2.15	Wildfires	0.010	0.000	0.000	0.000	0.000	0.000	
t2.16	Erosion	0.000	0.061	0.319	0.011	0.028	0.109	
t2.17	Depop	0.069	0.029	0.000	0.027	0.041	0.000	
t2.18	Roads	0.000	0.000	0.459	0.016	0.029	0.159	
t2.19	Buildings	0.000	0.017	0.367	0.027	0.155	0.201	
t2.20	VCF	0.000	0.028	0.018	0.000	0.024	0.023	
t2.21	NDVI	0.134	0.093	0.000	0.006	0.074	0.000	

Codes for explanatory variables are given in Table 1

exhibited a similar behavior: southness and TPI, but also slope, soil depth, and soil temperature class were associated to high presence probability, while road and building densities produced a low presence probability (Figure S2b).

The ensemble models were successfully cross-validated ($AUC=0.865$ for pine and 0.944 for oak) and correctly predicted most observations (sensitivity=83.4 and 96.9 %, specificity=72.7 and 80.9 %, respectively) (Fig. 2). Residuals were immune from spatial autocorrelation and trends against any of the predictors.

In 2080 (SRES A1B emission scenario, continuing population trend), the mean probability of occurrence of Scots pine declined slightly (0.33 vs. a current 0.36 across the whole study area) (Fig. 3). However, it increased under the intense land use scenario (0.45) (Fig. 4). The area with a probability of occurrence of Scots pine >0.6 decreased from 8700 to 8000 ha under the climate warming scenario and increased to 8800 ha under climate warming intense land use. The probability of occurrence of Scots pine always declined at lower elevations and increased at higher ones (Fig. 5); mean elevation of simulated presence points shifted from 1328 to 1528 m a.s.l. under climate warming and to 1473 m a.s.l. under climate warming intense land use, i.e., an upward shift of the potential niche of 200 and 145 m, respectively.

Oak increased its probability of occurrence under all scenarios (6100 ha under current conditions, 10,100 ha under climate change only, and 14,700 ha under climate change intense land use). Mean elevation of simulated presence points (probability of occurrence >0.6) shifted from 705 to 922 and 933 m a.s.l., respectively, i.e., an upward shift of 215 and 222 m.

The area of Scots pine pixels classified as decline was 147 in year 2003 and 102 in year 2006. However, in neither year, we observed a significant difference between decline and non-decline pixels in the modeled probability of occurrence of Scots pine (Fig. 6).

4 Discussion

Many processes are at work in determining pine decline. Drought is either a direct or a predisposing factor of mortality (Rebetez and Dobbertin 2004; Choat et al. 2013); also, land use change may eventually result in competitive exclusion of light-demanding Scots pine, and at low elevations, Scots pine reaches more rapidly decay stages, since trees weakened by drought are easily killed by “inciting” or “contributing” biotic agents (Dobbertin et al. 2005; Bigler et al. 2006; Vacchiano et al. 2012).

Climate warming and drought are related (i.e., the frequency of drought spells is expected to increase under climate change: Allen et al. 2010); however, extreme drought events may be more important than average climate trends in determining plant population viability and distribution (Katz and Brown 1992; Bréda and Badeau 2008), and they can induce shifts in species composition and distribution (Jentsch et al. 2007). Published models of Scots pine distribution under scenarios of climate change have produced contrasting results (e.g., Casalegno et al. 2011; Meier et al. 2011), probably as a result of different datasets and processes being included or not in the models (e.g., dispersal constraints, biotic competition, choice of climate, and drought-related variables).

In order to take into account the different factors governing drought sensitivity, we included in our models its meteorological, topographic, and soil-related component. At the resolution and extent analyzed, the probability of occurrence of Scots pine increased under climatic and topographic aridity. This is consistent with the biogeography of the species that forms pure stands in most inner-Alpine valleys such as the study area, preferentially on south-facing slopes and ridge positions (Ozenda 1985). Accordingly, low aridity reduced the probability of presence of Scots pine. In Aosta valley, temperature and precipitation are strongly correlated to elevation (which for this reason was excluded from the analysis); therefore, the AI variable contained also information regarding the upper elevational limits of the habitat suitable for Scots pine.

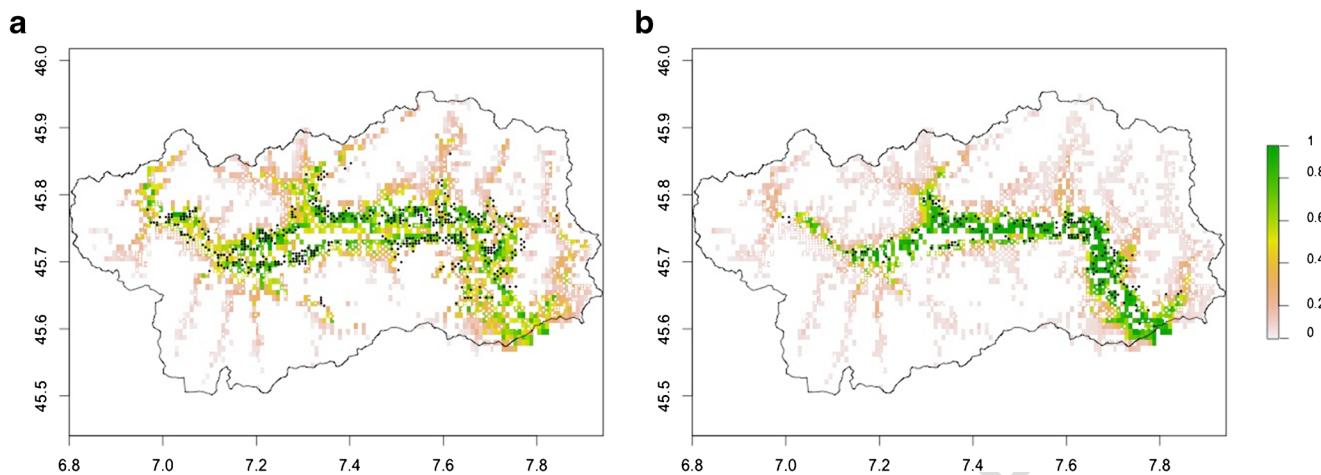


Fig. 2 Occurrence probability (0–1) of **a** Scots pine and **b** downy oak under current climate. Ensemble model (mean of GLM, MARS, and ANN). Presence points from the regional forest inventory in black

502 Another important driver of Scots pine occurrence was
 503 biotic competition, as expressed by NDVI of the forest canopy.
 504 As expected, the early seral pine cannot establish successfully
 505 under thick canopy cover (Vickers 2000). In contrast, it
 506 can also establish successfully on non-forested land, such as
 507 abandoned pastures and meadows (Poyatos et al. 2003), but
 508 this process could not be taken into consideration in future
 509 simulations, since our correlative models were calibrated on
 510 current vegetation conditions only.

511 In addition to topo-climatic and competition variables that
 512 are routinely assessed in SDM, we also evaluated the effect of
 513 soil properties (albeit using a coarse resolution and dummy
 514 coding) and natural and anthropogenic disturbances (Matias
 515 and Jump 2012). Scots pine did not exhibit any soil preference,
 516 consistently with its edaphic plasticity (Médail 2001). However,
 517 its occurrence was moderately associated to the absence of steep slopes and severe land erosion, which should
 518 be adverse to permanent vegetation cover, and to recurring
 519 wildfires. Wildfire polygons were not labeled as surface or
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521 crown fires; however, surface fires are more common in the
 522 study area, especially at low elevations on south-facing slopes
 523 (Vacchiano et al. 2013).

524 We also evaluated the effect of human land use on species
 525 distribution by using proxy variables (Garbarino et al. 2009).
 526 Increased population and road density resulted in increased
 527 occurrence of Scots pine. Management practices such as tim-
 528 ber harvesting, litter collection, and forest grazing may in fact
 529 prevent succession to more competitive late-seral species
 530 (Weber et al. 2008; Gimmi et al. 2010). The association
 531 between pine and population/road density may also be due
 532 to recent establishment of Scots pine after agricultural aban-
 533 donment (Poyatos et al. 2003). Building density was nega-
 534 tively correlated to the probability of occurrence of both Scots
 535 pine and downy oak, likely due to the spatial segregation of
 536 forests vs. developed or urbanized areas in the main valley.

537 These factors help explain the response of Scots pine
 538 distribution in 2080 under the A1B warming scenario, i.e., a
 539 modest reduction of habitat suitability, but a significant

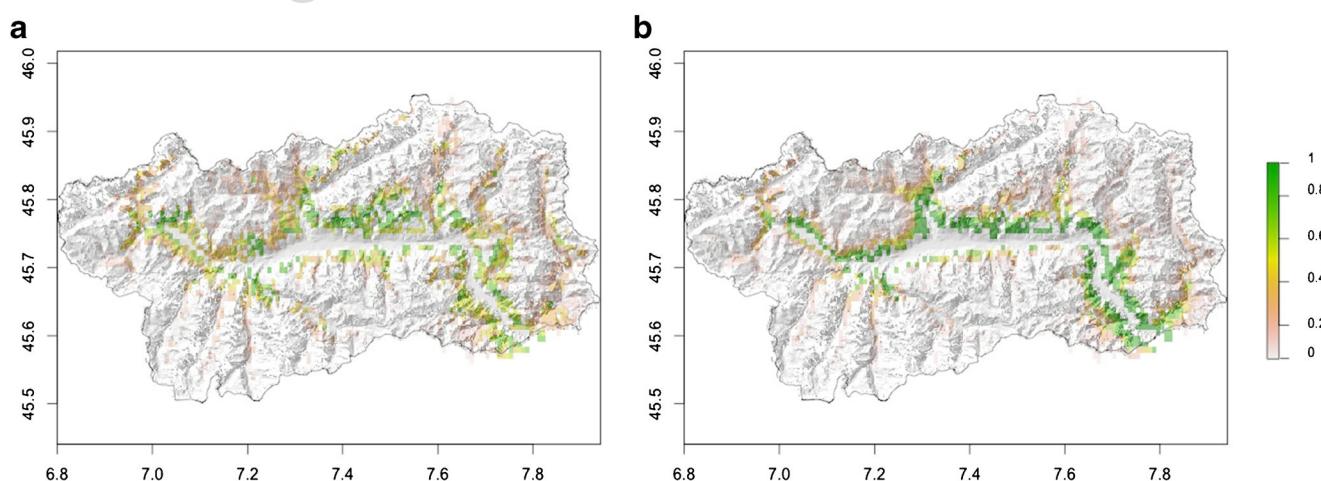


Fig. 3 Occurrence probability (0–1) of **a** Scots pine and **b** downy oak under 2080 climate and current land use scenario. Ensemble model (mean of GLM, MARS, and ANN)

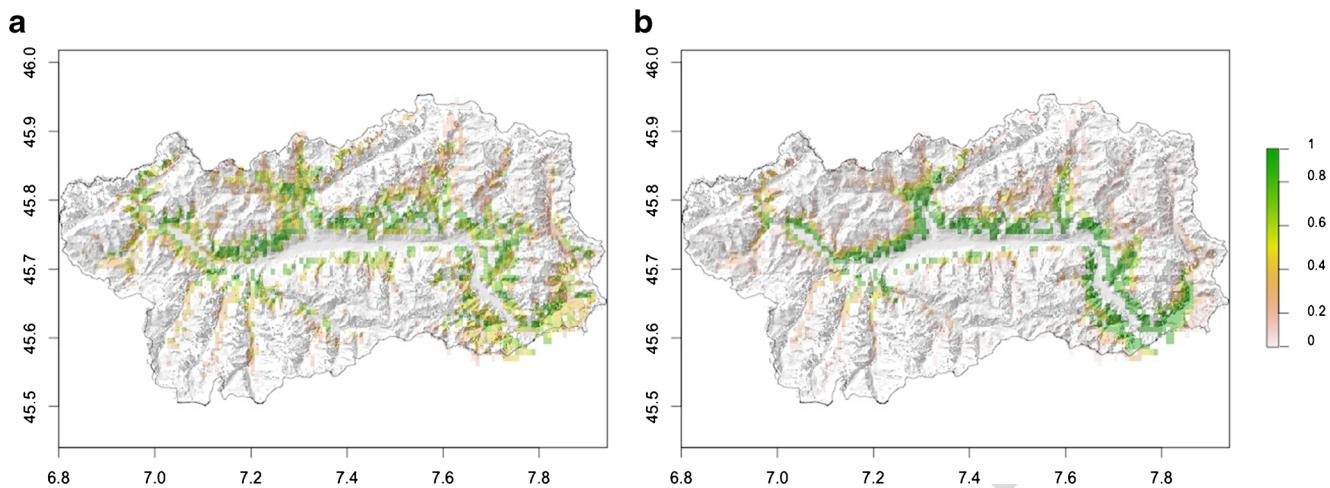


Fig. 4 Occurrence probability (0–1) of **a** Scots pine and **b** downy oak under 2080 climate and intensive land use scenario. Ensemble model (mean of GLM, MARS, and ANN)

540 increase of its optimum elevation. At low elevations, in fact,
541 aridity could reach the lower limits for the species to persist, as

suggested by the MARS response curve (Garzon et al. 2008).
542 This change is partially counteracted in a scenario where land
543

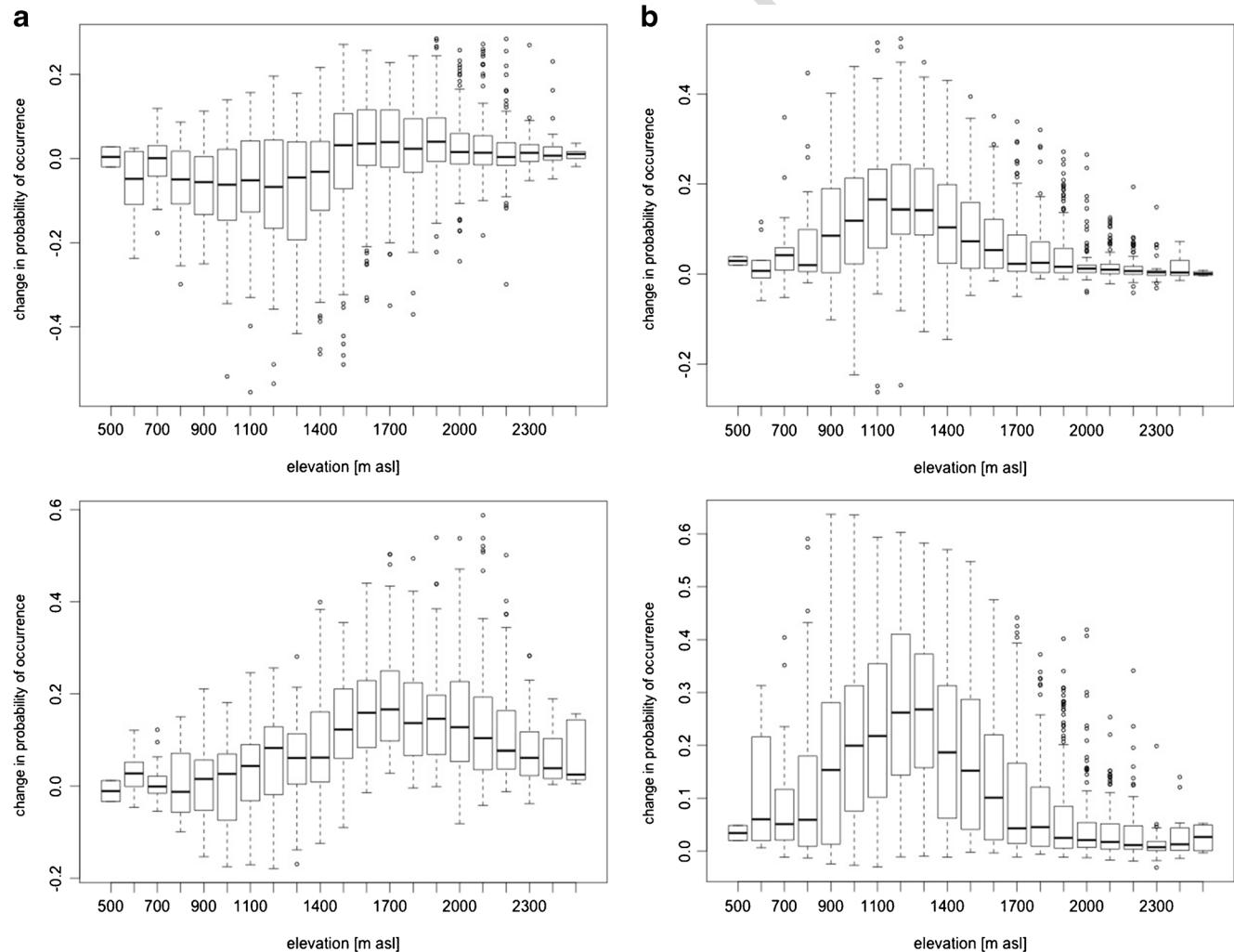
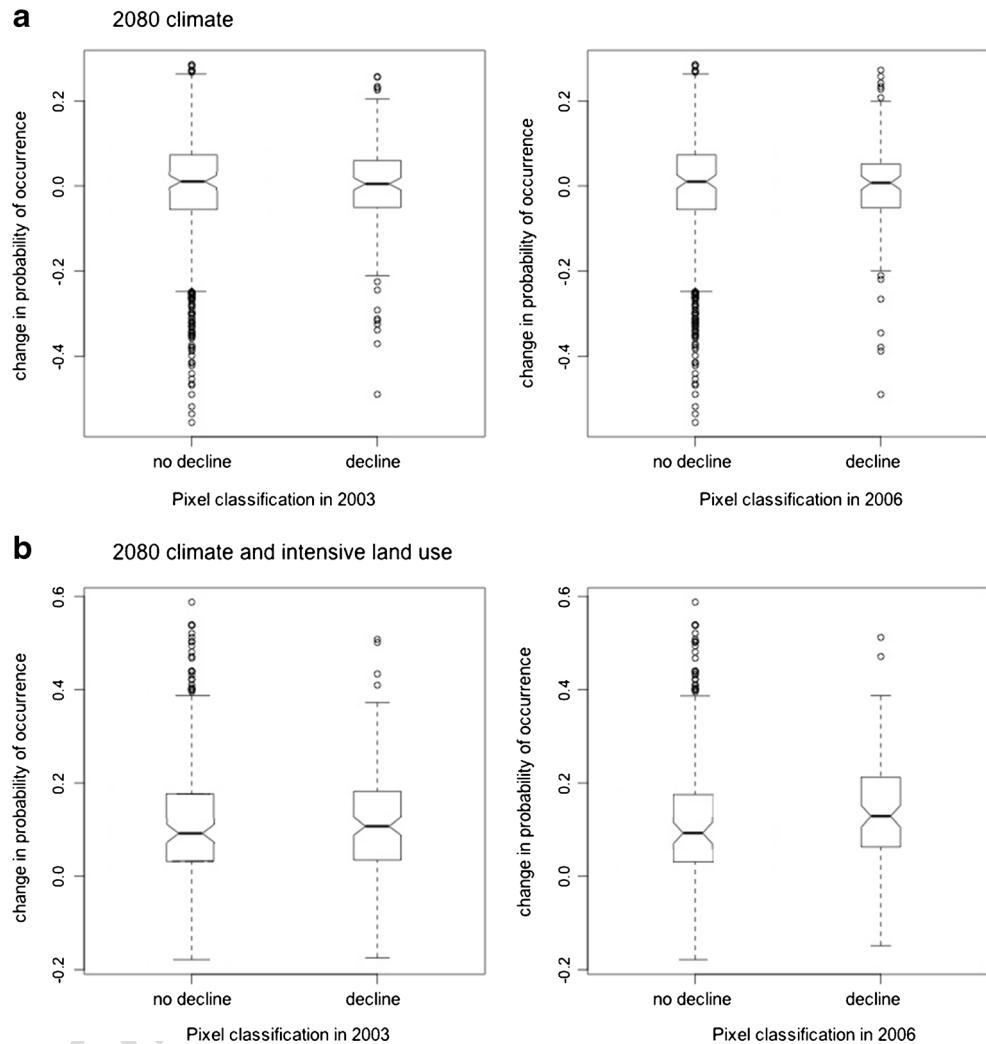


Fig. 5 Change in probability of occurrence (2080–current) of **a** Scots pine and **b** downy oak for different elevation classes under 2080 climate (*above*) and 2080 climate intensive land use scenario (*below*)

Fig. 6 Change in probability of occurrence (2080–current) of Scots pine for decline and non-decline pixels in dry years 2003 (left) and 2006 (right), under 2080 climate (above) and 2080 climate intensive land use scenario (below)



abandonment is prevented from occurring: in this case, the probability of occurrence of Scots pine would still decrease at low elevations but, on average, the human factor could be sufficient to prevent the decline of Scots pine throughout its current distribution. This analysis is correlative and does not explore the physiological and successional processes behind such land use/climate change tradeoff. However, it is indicative of the fact that land use changes can be as strong as climate change in determining future species composition and dominance of mountain forests (Dirnböck et al. 2003) and that they deserve a deeper attention in modeling species' response to future climate conditions.

The distribution of downy oak shared the same topoclimatic features as Scots pine (high aridity/low elevation, southern aspects, low erosion, high soil temperature) but was also associated to lower land use intensity (road density) and higher soil depth. Canopy density (NDVI) and natural disturbances were not influential, since downy oak is more shade-tolerant than pine (Monnier et al. 2013). The response

of downy oak to climate warming was different from Scots pine and produced an increased probability of occurrence throughout the study region. Previous research has demonstrated that downy oak is better adapted than Scots pine to both short- and long-term drought, due to its different physiological responses, i.e., stomata closure, resistance to embolism, and seedling vitality (Eilmann et al. 2006; Poyatos et al. 2008; Morán-López et al. 2012).

Population change was not among the most important predictors of current downy oak distribution. However, we detected a moderate association between population increase and higher probability of occurrence of oak. This can be due either to the practice of coppicing oaks for firewood or to the fact that depopulated areas are located in the remotest part of lateral valleys, where elevation and sites are far below optimum for downy oak.

The use of ensemble modeling is justified by the need to reduce model uncertainty due to different modeling approaches (Marmion et al. 2003). Ensemble models in

582 biomod2 are obtained by averaging model prediction and
 583 excluding models with low predictive power ($AUC < 0.75$);
 584 model predictions are weighted by the AUC of their respective
 585 modeling approach. In this study, all three model approaches
 586 produced an $AUC > 0.75$. However, differences in importance
 587 of explanatory variables and shape of response curves were
 588 apparent. MARS are more flexible than GLM as they are fit
 589 using piecewise linear splines and are particularly useful when
 590 assuming that the shape of species' responses is not linear
 591 (Leathwick et al. 2005). ANN, on the other hand, are not
 592 based on specific distribution functions of the response. They
 593 are robust to noisy and non-linear responses and allow for
 594 categorical predictors (such as soil characteristics in this
 595 study). Therefore, they are particularly appropriate in an ex-
 596 ploratory context. On the other hand, they are sensitive to
 597 multicollinearity and prone to overfitting, and interpretation of
 598 causal relationships for individual predictors is not straight-
 599 forward (Manel et al. 1999). The differences are apparent in
 600 species response curves (Figure S2), with MARS and ANN
 601 capable of detecting non-linear responses to some explanatory
 602 variables that were not picked up by GLM, despite a similar
 603 predictive performance. This is reflected by the higher impor-
 604 tance of some explanatory variables, such as roads, buildings,
 605 TPI, or erosion, under models capable of detecting non-linear
 606 species responses (Table 2).

607 Finally, contrary to our expectations, we did not detect any
 608 overlap between drought-induced Scots pine decline in years
 609 2003 and 2006 and change in occurrence probability under a
 610 warming scenario. Widespread tree mortality can occur under
 611 extreme dry spells, but it is uncertain whether one or two
 612 extreme years are sufficient to trigger major shifts in forest
 613 composition (e.g., Vicente-Serrano et al. 2013). The effect of
 614 extreme years on the realized niche of Scots pine will likely
 615 depend on the frequency and severity of droughts, rather than
 616 on decadal climate means such as the ones we used in our
 617 projections. Other parameters might be important in their
 618 extreme yearly or seasonal values, such as high precipitation
 619 events promoting a new generation after a mortality episode
 620 (Matias and Jump 2012), late frost preventing uphill expan-
 621 sion of sensitive species such as downy oak (Burnand 1976),
 622 and natural disturbances such as large, stand-replacing fires
 623 (Moser et al. 2010).

624 What is certain, however, is that downy oak is equipped
 625 with better adaptations to drought and is likely to replace Scots
 626 pine at lower elevations under a warming scenarios, whereby
 627 an increased frequency of droughts is to be expected (Dai
 628 2012). Management actions have the potential to mitigate this
 629 shift (Vilà-Cabrera et al. 2013), e.g., thinning to 40–60 %
 630 initial basal area to mitigate drought effects on Scots pine on
 631 xeric sites (Giuggiola et al. 2013). However, effects of man-
 632 agement actions must be more thoroughly explored to eval-
 633 uate tradeoffs with each species' resistance and resilience in the
 634 face of climate forcing.

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