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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		Division	Dipartimento di Scienze Agrarie, Forestali e Alimentari
11		Address	Largo Braccini 2, Grugliasco 10095, TO, Italy
12		e-mail	gvacchiano@gmail.com
13		Family Name	Motta
14		Particle	
15		Given Name	Renzo
16		Suffix	
17	Author	Organization	Università degli Studi di Torino
18		Division	Dipartimento di Scienze Agrarie, Forestali e Alimentari
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Electronic supplementary material

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

Giorgio Vacchiano · Renzo Motta

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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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G. Vacchiano (✉) · R. Motta
Dipartimento di Scienze Agrarie, Forestali e Alimentari, Università degli Studi di Torino, Largo Braccini 2, 10095 Grugliasco, TO, Italy
e-mail: gvacchiano@gmail.com

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 abandon-
 72 ment of traditional land use practices. Under such scenario,
 73 succession by mid-tolerant species such as downy oak
 74 (*Quercus pubescens* Willd.) is favored over Scots pine regener-
 75 ation (Urbietta 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 Recession 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 $-1\text{ }^{\circ}\text{C}$ (mean temperature of the coldest month) and $+33\text{ }^{\circ}\text{C}$
 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 ($-90\text{ }^{\circ}\text{C}$:
 115 Sakai and Okada 1971).

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

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

2.2 Study area

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

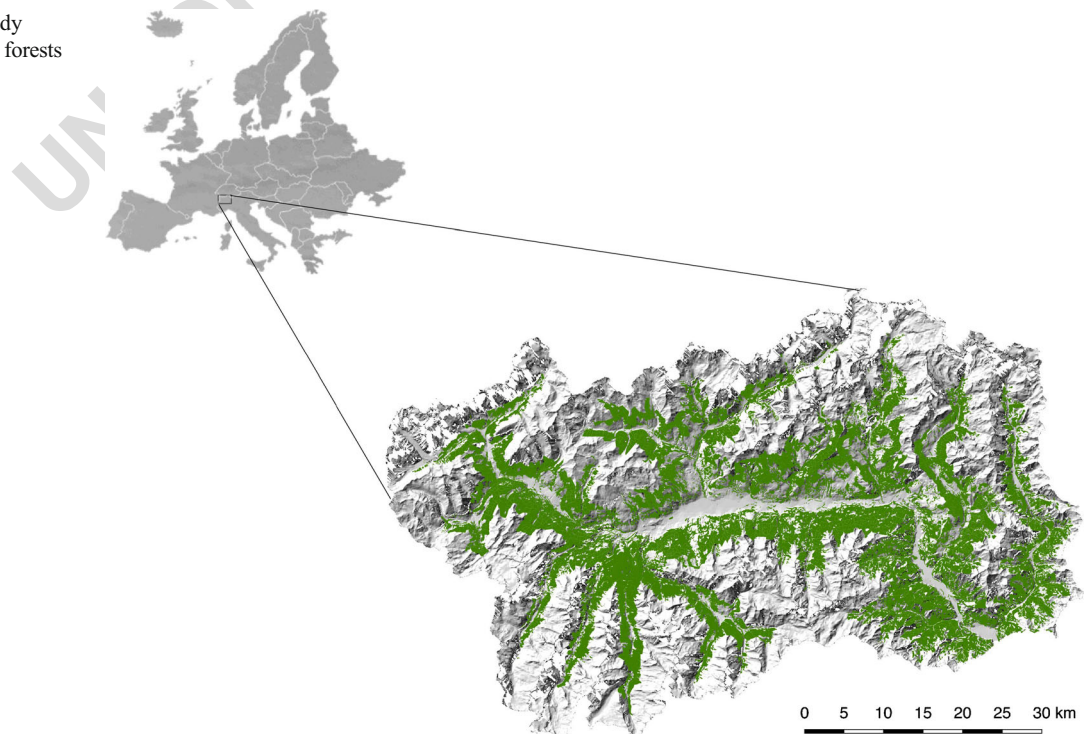
175 Scots pine stands in the study area cover 5372 ha
 176 (Gasparini and Tabacchi 2011), i.e., 6 % of the total forest
 177 area, and thrive on both acidic and basic substrates of well-
 178 exposed, bottom to mid-elevation slopes. Stands dominated
 179 by Scots pine are mostly young, averaging 920 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 210

211 In order to model the occurrence of Scots pine and downy oak
 212 in the study area, we used a diverse set of explanatory vari-
 213 ables including vectorial as well as raster information at dif-
 214 ferent spatial resolutions. All variables were resampled at a
 215 common spatial resolution of 1 km, i.e., the coarsest resolution
 216 among all explanatory variables, and clipped to a land use
 217Q9 mask of current forest distribution. In fact, we decided to
 218 exclusively include presence/absence of pine and oak in areas

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).

$$RAD_i(TMEAN_i + 17.8) \frac{(TMAX_i - TMIN_i)}{2} \text{ days}$$

- 244
 245
 246 (3) Soil variables at a 1-km resolution, extracted from the
 247 European Soil database (European Soil 1999). We se-
 248 lected variables potentially important for tree establish-
 249 ment and growth, namely available water capacity
 250 (*AWC*) of the topsoil, accumulated soil temperature class
 251 (*ATC*), total organic carbon (*OC*) of the topsoil, base
 252 saturation (*BS*), erodibility (*ERO*), depth to rock (*DR*),
 253 dominant surface textural class (*TEXT*), and volume of
 254 stones (*VS*). All variables were coded as dummy values.
 255 (4) Natural disturbances, such as landslides or severe soil
 256 erosion (source: Corine Land Cover 1990 raster cover-
 257 age, resolution 500 m), avalanche tracks, and wildfires
 258 >10 ha for the years 1961–1991 (sources: Regione
 259 Autonoma Valle d’Aosta, Ufficio Neve e Valanghe, and
 260 Regione Autonoma Valle d’Aosta, Corpo Forestale
 261 Regionale, Nucleo Antincendo Boschivi).
 262 (5) Competition by the pre-existing canopy, assessed by
 263 extracting the Normalized Difference Vegetation Index
 264 (*NDVI*) from a Landsat 5 Thematic Mapper image (path
 265 195, row 28) taken on June 30, 1987 (resolution 30 m).
 266 The acquisition period was chosen as to be at the peak at
 267 the growing season; the image had 10 % cloud cover, but

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. 289

2.4 Model runs under future scenarios 290

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

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

317 population change using figures for the period 1951– 367
 318 1991 and (2) maintenance of high land use, i.e., all 368
 319 municipalities were assigned 0 % variation in population 369
 320 respective to 1951, thereby assuming a continued pres- 370
 321 ence of man and its activities at all rural settings.

322 Soil characteristics are also responsive to climate change 371
 323 (Singh et al. 2011); however, we kept these variables at current 372
 324 conditions for the 2080 simulation, since no quantitative sce- 373
 325 narios are available to estimate future changes. Altogether, 374
 326 three scenarios were simulated: current conditions, 2080 cli- 375
 327 mate with unchanged land use, and 2080 climate with intense 376
 328 land use.

329 2.5 Model building 377

330 Presence/absence of pine and oak in the years 1992–1994 378
 331 served as a response variable, which we extracted from a 379
 332 regional forest inventory based on a 500-m regular grid. At 380
 333 every grid node, the species and diameter at breast height 381
 334 (DBH) of each living tree (DBH >7.5 cm) were measured 382
 335 within a variable-radius circular plot (radius 8–15 m depend- 383
 336 ing on tree density). Plot coordinates were recorded to the 384
 337 nearest meter. Scots pine and downy oak were labeled as 385
 338 present where at least one tree of each species was recorded 386
 339 and absent otherwise. 387

340 We assumed that both pine and oak distribution are in 388
 341 equilibrium with the environment (Rohde 2005). For this 389
 342 reason, and because our aim was to model potential niche, 390
 343 no migration constraints were included in the model. 391

344 We used an ensemble modeling approach (Araujo and New 392
 345 2007), by fitting and averaging predictions obtained by a 393
 346 generalized linear model (GLM), artificial neural network 394
 347 (ANN), and multiple adaptive regression spline (MARS) 395
 348 using the same set of responses, predictors, and scenarios. 396
 349 Model specifications were as follows: (a) for GLM, a back- 397
 350 ward stepwise algorithm was used, based on Akaike Informa- 398
 351 tion Criterion (AIC); (b) for ANN, the initial number of cross- 399
 352 validations to find best size and decay parameters was set to 400
 353 five; and (c) for MARS, the cost per degree of freedom charge 401
 354 was set to 2, and the model was pruned in a backward stepwise 402
 355 fashion. All models were fit on a binomial distribution with 403
 356 logit link, without interactions between predictors, and using a 404
 357 maximum of 100 iterations. 405

358 For each of the three models, we computed variable impor- 406
 359 tance ratings and response curves. To do so, all variables but 407
 360 one are set constant to their median value, and only the remain- 408
 361 ing one is allowed to vary across its whole range. In the case of 409
 362 categorical variables (e.g., soil), the most represented class was 410
 363 used. The variations observed and the curve thus obtained show 411
 364 the sensibility of the model to that specific variable. 412

365 We carried out *k*-fold cross-validation of the model by 413
 366 subdividing the data into a 3:1 proportion (*k*=4). Model 414

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

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

2.6 Effect of extreme drought events 388

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

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

3 Results 408

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

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	<i>AI</i>	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	<i>Slope</i>	Slope from DTM	0–44	17.0	°	10 m
t1.16	<i>TPI</i>	Topographic position Index	-3.0–3.1	-0.4	-	10 m
t1.17	<i>Southness</i>	Linearization of aspect	0–180	97.2	°	10 m
t1.18	<i>ATC</i>	Accumulated Soil temperature class ^c	1–3	-	Dummy	1 km
t1.19	<i>AWC</i>	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	<i>DR</i>	Soil depth to rock ^c	1–4	-	Dummy	1 km
t1.22	<i>ERO</i>	Soil erodibility ^c	3–5	-	Dummy	1 km
t1.23	<i>OC</i>	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	<i>VS</i>	Volume of stones in the soil ^c	0–2	-	Dummy	1 km
t1.26	<i>Avalanches</i>	Number of avalanche polygons ^b	0–3	0.1	Count	10 m
t1.27	<i>Wildfires</i>	Number of fire polygons, 1961–1990 ^b	0–3	0.0	Count	10 m
t1.28	<i>Erosion</i>	Total area subject to landslide or erosion ^d	0–14,523	656.9	m ²	500 m
t1.29	<i>Depop</i>	Change in population 1951–1991 ^e	-59–135	2.1	% change	Municipality
t1.30	<i>Roads</i>	Total road length ^b	0–8485	1812.0	m	500 m
t1.31	<i>Buildings</i>	Total buildings area ^b	0–40,190	1591.8	m ²	500 m
t1.32	<i>VCF</i>	Tree cover from Landsat (2001) ^f	0–99	29.9	%	30 m
t1.33	<i>NDVI</i>	NDVI from Landsat (1987)	0.20–0.66	0.30	0–1	30 m

Explanatory variables in species distribution models are set in italics

^a Hijmans et al. (2005)

^b Regione Autonoma Valle d'Aosta

^c European Soil (1999)

^d European Environment (2013)

^e ISTAT (2012)

^f Sexton 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 tempera-
417 ture, $R=0.993$ vs. annual precipitation, $R=-0.962$ vs. GDD).

418 AI was the most important predictor for the current distri-
419 bution 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	t2.3 Variable	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
t2.5	Slope	0.000	0.086	0.006	0.038	0.087	0.023
t2.6	TPI	0.145	0.162	0.000	0.099	0.103	0.000
t2.7	Southness	0.180	0.393	0.283	0.210	0.269	0.220
t2.8	ATC	0.000	0.017	0.000	0.078	0.042	0.000
t2.9	AWC	0.000	0.000	0.000	0.000	0.000	0.000
t2.10	DR	0.000	0.000	0.000	0.251	0.138	0.000
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

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

433 The ensemble models were successfully cross-validated
 434 (AUC=0.865 for pine and 0.944 for oak) and correctly pre-
 435 dicted most observations (sensitivity=83.4 and 96.9 %, spec-
 436 ificity=72.7 and 80.9 %, respectively) (Fig. 2). Residuals
 437 were immune from spatial autocorrelation and trends against
 438 any of the predictors.

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

Oak increased its probability of occurrence under all sce- 453
 narios (6100 ha under current conditions, 10,100 ha under 454
 climate change only, and 14,700 ha under climate change 455
 intense land use). Mean elevation of simulated presence points 456
 (probability of occurrence >0.6) shifted from 705 to 922 and 457
 933 m a.s.l., respectively, i.e., an upward shift of 215 and 458
 222 m. 459

The area of Scots pine pixels classified as decline was 147 460
 in year 2003 and 102 in year 2006. However, in neither year, 461
 we observed a significant difference between decline and non- 462
 decline pixels in the modeled probability of occurrence of 463
 Scots pine (Fig. 6). 464

4 Discussion 465

Many processes are at work in determining pine decline. 466
 Drought is either a direct or a predisposing factor of mortality 467
 (Rebetez and Dobbertin 2004; Choat et al. 2013); also, land 468
 use change may eventually result in competitive exclusion of 469
 light-demanding Scots pine, and at low elevations, Scots pine 470
 reaches more rapidly decay stages, since trees weakened by 471
 drought are easily killed by “inciting” or “contributing” biotic 472
 agents (Dobbertin et al. 2005; Bigler et al. 2006; Vacchiano 473
 et al. 2012). 474

Climate warming and drought are related (i.e., the frequen- 475
 cy of drought spells is expected to increase under climate 476
 change: Allen et al. 2010); however, extreme drought events 477
 may be more important than average climate trends in deter- 478
 mining plant population viability and distribution (Katz and 479
 Brown 1992; Bréda and Badeau 2008), and they can induce 480
 shifts in species composition and distribution (Jentsch et al. 481
 2007). Published models of Scots pine distribution under 482
 scenarios of climate change have produced contrasting results 483
 (e.g., Casalegno et al. 2011; Meier et al. 2011), probably as a 484
 result of different datasets and processes being included or not 485
 in the models (e.g., dispersal constraints, biotic competition, 486
 choice of climate, and drought-related variables). 487

In order to take into account the different factors governing 488
 drought sensitivity, we included in our models its meteorolog- 489
 ical, topographic, and soil-related component. At the resolution 490
 and extent analyzed, the probability of occurrence of Scots pine 491
 increased under climatic and topographic aridity. This is con- 492
 sistent with the biogeography of the species that forms pure 493
 stands in most inner-Alpine valleys such as the study area, 494
 preferentially on south-facing slopes and ridge positions 495
 (Ozenda 1985). Accordingly, low aridity reduced the probabili- 496
 ty of presence of Scots pine. In Aosta valley, temperature and 497
 precipitation are strongly correlated to elevation (which for this 498
 reason was excluded from the analysis); therefore, the AI 499
 variable contained also information regarding the upper 500
 elevational limits of the habitat suitable for Scots pine. 501

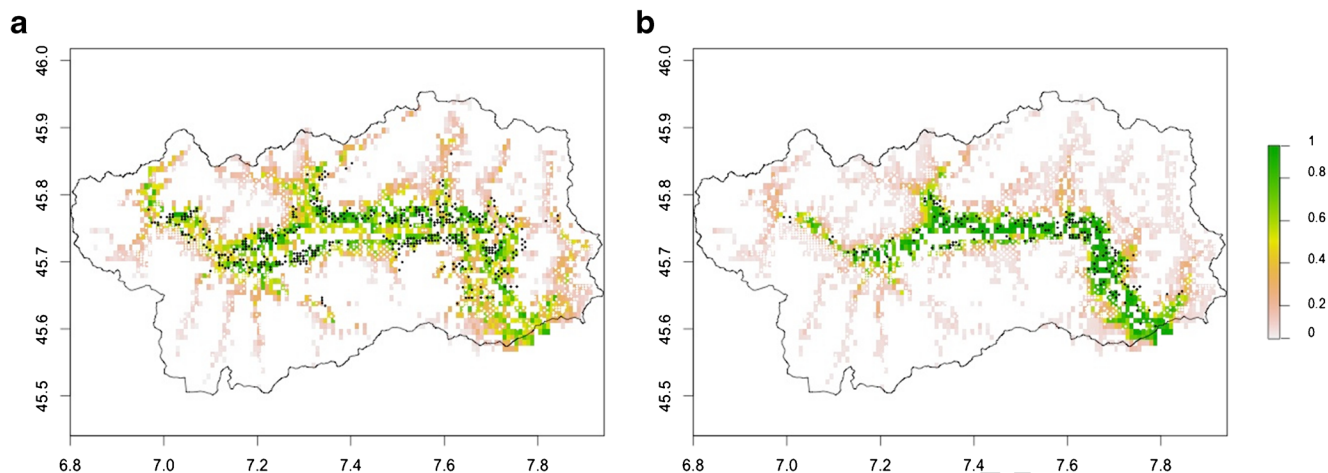


Fig. 2 Occurrence probability (0–1) of **a** Scots pine and **b** downy oak under current climate. Ensemble model (mean of GLM, MARS, and ANN). Presence points from the regional forest inventory *in black*

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 success-
 505 fully 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 prefer-
 516 ence, consistently with its edaphic plasticity (Médail 2001).
 517 However, its occurrence was moderately associated to the
 518 absence of steep slopes and severe land erosion, which should
 519 be adverse to permanent vegetation cover, and to recurring
 520 wildfires. Wildfire polygons were not labeled as surface or

521 crown fires; however, surface fires are more common in the 521
 522 study area, especially at low elevations on south-facing slopes 522
 523 (Vacchiano et al. 2013). 523

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

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

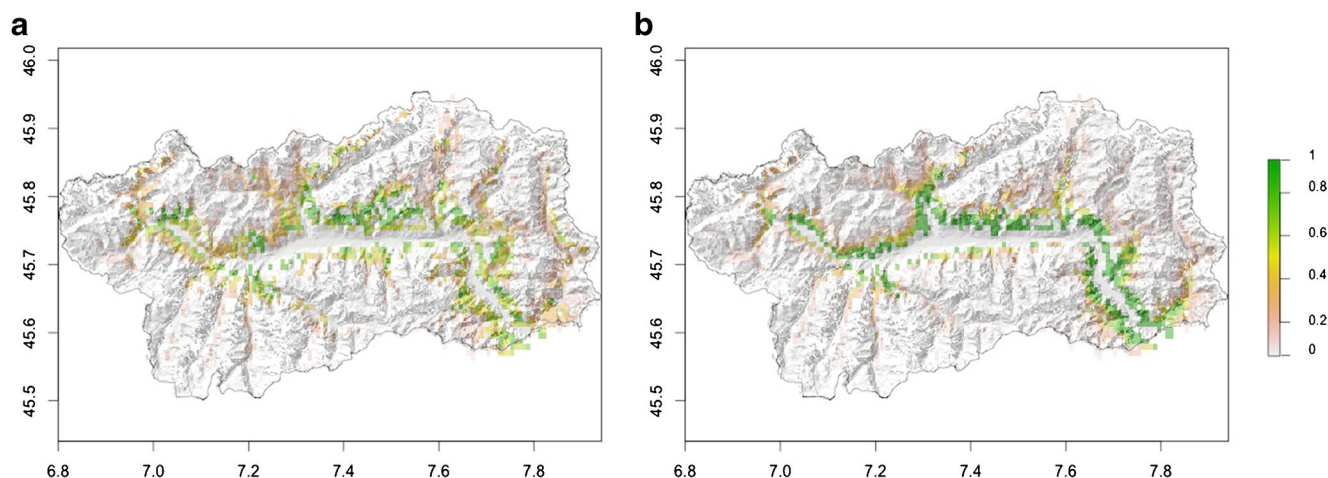


Fig. 3 Occurrence probability (0–1) of **a** Scots pine and **b** downy oak under 2080 climate and current land use scenario. Ensemble model (mean of GLM, MARS, and ANN)

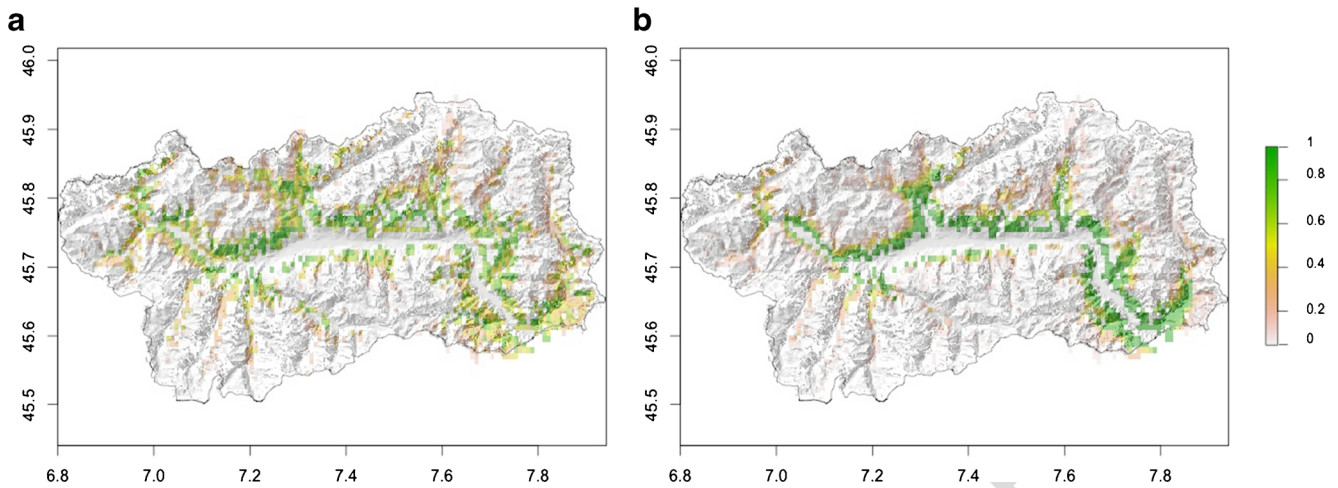


Fig. 4 Occurrence probability (0–1) of **a** Scots pine and **b** downy oak under 2080 climate and intensive land use scenario. Ensemble model (mean of GLM, MARS, and ANN)

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

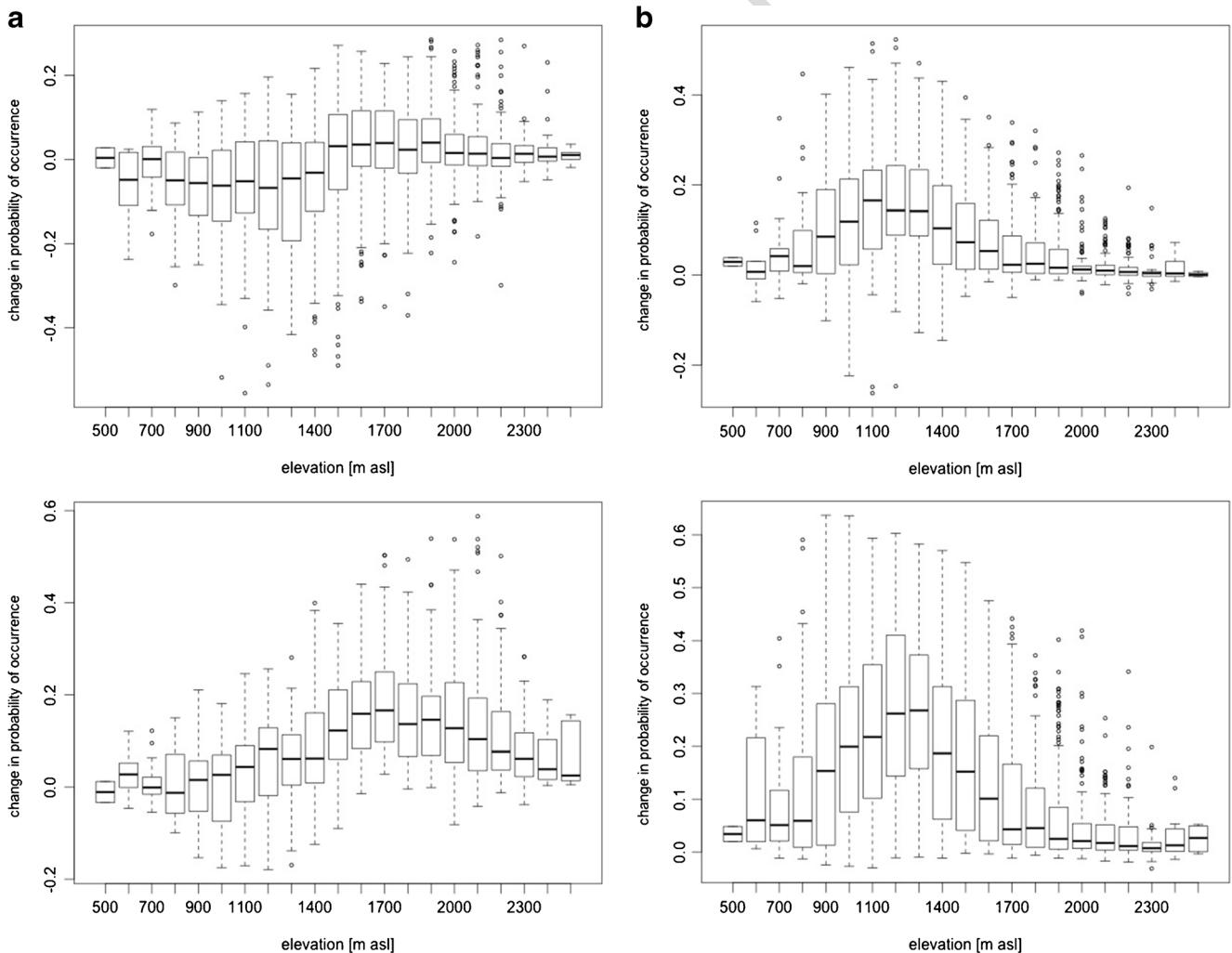
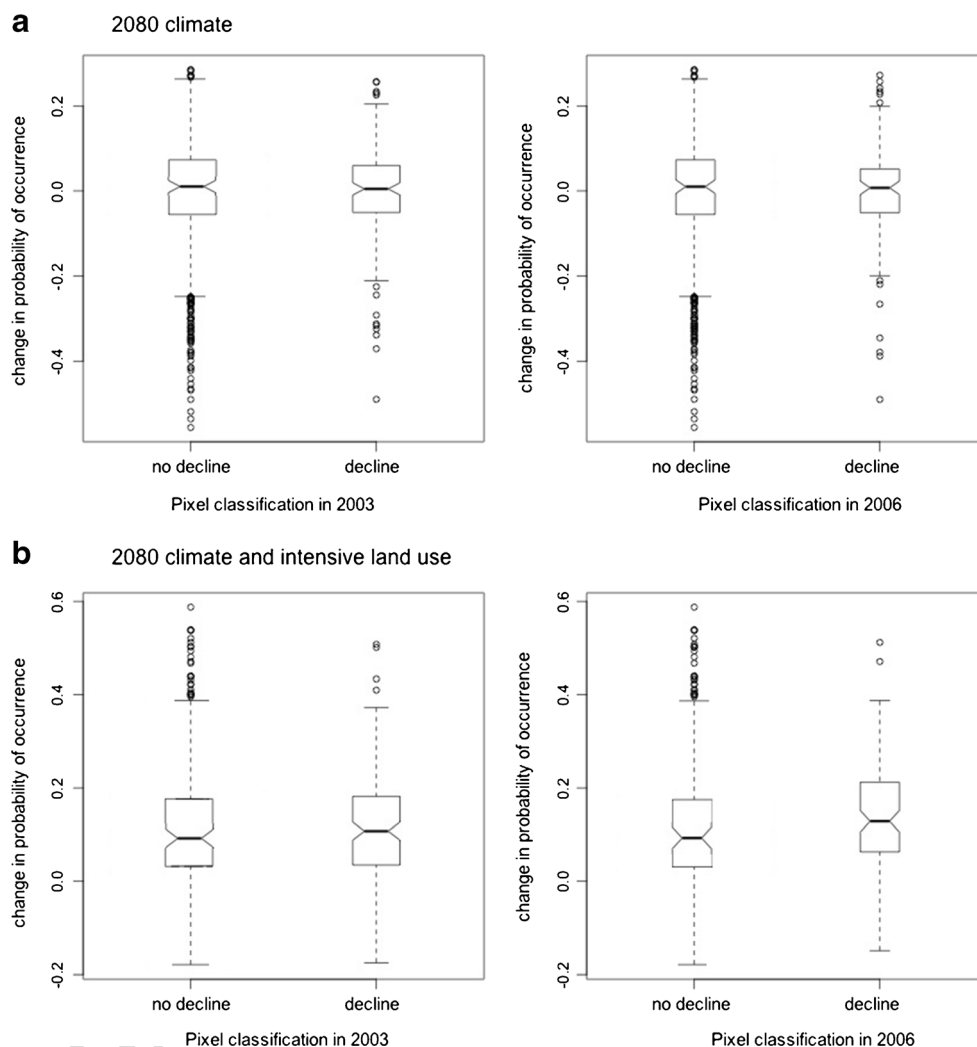


Fig. 5 Change in probability of occurrence (2080–current) of **a** Scots pine and **b** downy oak for different elevation classes under 2080 climate (*above*) and 2080 climate intensive land use scenario (*below*)

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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)



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

556 The distribution of downy oak shared the same topo-
 557 climatic features as Scots pine (high aridity/low elevation,
 558 southern aspects, low erosion, high soil temperature) but
 559 was also associated to lower land use intensity (road density)
 560 and higher soil depth. Canopy density (NDVI) and natural
 561 disturbances were not influential, since downy oak is more
 562 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 demon-
 strated that downy oak is better adapted than Scots pine to
 both short- and long-term drought, due to its different physi-
 ological responses, i.e., stomata closure, resistance to embo-
 lism, 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 opti-
 mum for downy oak.

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

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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 evalu-
 633 ate tradeoffs with each species' resistance and resilience in the
 634 face of climate forcing.

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