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

--Manuscript Draft--

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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 towards oak-dominated forests? What is the role of extreme drought years? Aims: determine drivers of current distribution of Scots pine and downy oak in Aosta valley (SW Alps); extrapolate species distribution models to year 2080 (SRES A1B); assess the ability of pine vitality response to the extreme droughts in 2003 and 2006 to predict modeled vegetation changes. Methods: ensemble distribution models using climate, topography, soil, competition, natural disturbances, and land use. Species presence was derived from a regional forest inventory. Pine response to drought of 2003-06 was assessed by 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.

Dear Editors,
please receive the second revised version of the manuscript "An improved species distribution model for Scots pine and Downy oak under future climate change in the NW Italian Alps", by me and prof. Renzo Motta.

This work was presented as a talk in the ClimTree 2013 conference in Zurich. I am aware that the submission is well after the deadline for the special issue of your journal. If it's not possible to include the paper in the special issue, please consider this a normal submission of a research paper.

The paper has not been previously submitted to any other journal. The main topic is the effect of climate change and drought on the regional distribution of Scots pine and Downy oak in northern Italy. Although only locally fit, the species distribution model has some unique features which we believe could be of interest to other researchers around the world, such as the inclusion of soil, natural disturbance, and biotic competition.

We also compared SDM predictions to the effect of two severe dry years on forest canopies assessed by remote sensing.

The paper has been revised again following indications by the Editor, which improved it in both clarity and succinctness.

We believe our methods and conclusions are of relevance to the readers of your journal, especially in the context of climate-related forest research.

We look forward to publish our work in your journal.
Sincerely,

the corresponding author
Giorgio Vacchiano

Line 82: Add 'it' before ‚was favored'
ADDED

Line 87–88: better: ‚Scots pine often forms stable communities due to limited competiveness of other conifer tree species.'
EDITED

Lines 132, 136, 138, 180, 199, 218, 220, 224, 235, 238, 439, 664, 677, 679, 681, 683, 686 Table 1: Replace '-' (hyphen) and '÷' by '–' (en-dash)
REPLACE

Line 162: replace ‚april' by ‚April' and 'september' by ‚September'
REPLACED

Line 197: delete '-'
DELETED

Line 239: 'meter' instead of 'm'?
EDITED

Line 268: Give a reference after;; Wiens et al. 2010? Just to be correct about the definition.
REFERENCE ADDED

Lines 294-295: it would be interesting to know with which simple climate variable (or elevation?) AI was best correlated (including a quantification, R2). Perhaps this information can be added in a short comment here;; I consider it a result, too. AI may be a rather sophisticated parameter, though better to understand by a closest relative.
ADDED: "Pearson's correlation between AI and Worldclim variables was always higher than 0.95 (e.g., R =-0.995 vs. mean annual temperature, R =0.993 vs. annual precipitation, R =-0.962 vs. GDD)."

Line 315: add 'to' between 'and 1473'
ADDED

Line 355: Improve the sentence by e.g. add 'In contrast, ...' before 'It can also'
EDITED

Lines 365–367: Please clarify here. Perhaps there is only a little thing missing here.
EDITED: "Wildfire polygons were not labeled as surface or crown fires; however, surface fires are more common in the study area, especially at low elevations on south-facing slopes".

Line 385: I prefer here a slash instead an en-dash
EDITED

Line 390: replace 'than' by 'as'
EDITED

Line 395: replace 'than' by 'from'
EDITED

Line 415: replace 'suc' by 'such'
EDITED

Lines 421–423: The sentence sounds to me unclear. ‚To cascade on' is presumably not correct. Please re- phrase this sentence.
EDITED: "This is reflected by the higher importance of some explanatory variables, such as Roads, Buildings, TPI, or Erosion, under models capable of detecting non-linear species responses".

Line 430: delete ',' before 'that'
DELETED

Lines 428-435: There is too much information in this long sentence. Please split into two sentences in order to clarify the different impacts.
EDITED: :"The effect of extreme years on the realized niche of Scots pine will likely depend on the frequency and severity of droughts, rather than on decadal climate means such as the ones we used in our projections. Other parameters might be important in their extreme yearly or seasonal values, such as high precipitation events promoting a new generation after a mortality episode…".

Line 441: What is meant by 'their'? If management is meant, then write ,effects of management actions' to clarify this important sentence.
EDITED

Literature- Check for consistent abbreviations of all journal titles.
ALL CHECKED AND EDITED WHERE NEEDED

Line 666: add 'given' after 'are'
ADDED

Table 1: Check for citations Corine land Cover (1990) and ISTAT (2012). They are only referenced in the text. I propose nevertheless to reference them in the Literature section.
TWO REFERENCES ADDED

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

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Short title: Drought and distribution of Scots pine and downy oak

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Contribution of the coauthors: GV designed the study, conducted the analysis and wrote the paper. RM supervised the work and revised the manuscript.

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

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 towards oak-dominated forests? What is the role of extreme drought years?

Aims: determine drivers of current distribution of Scots pine and downy oak in Aosta valley (SW Alps); extrapolate species distribution models to year 2080 (SRES A1B); assess the ability of pine vitality response to the extreme droughts in 2003 and 2006 to predict modeled vegetation changes.

Methods: ensemble distribution models using climate, topography, soil, competition, natural disturbances, and land use. Species presence was derived from a regional forest inventory. Pine response to drought of 2003-06 was assessed by 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.

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. 2011), cambial activity (Eilmann et al. 2011; Oberhuber et al. 2011), hydraulic capacity (Sterck et al. 2008), and the likelihood of xylem cavitation (Martinez-Vilalta and Pinol 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. 2012).

On top of this, at the landscape level Scots pine forests in southern Europe have recently experienced a decrease in management intensity, shifting from open-canopy, even-aged stands maintained by broadleaves coppicing, wood pasture, litter raking, and pitch collection (Gimmi et al. 2007), to denser forests following depopulation of mountain areas and abandonment of traditional land-use practices. Under such scenario, succession by mid-tolerant species such as downy oak (*Quercus pubescens* Willd.) is favored over Scots pine regeneration (Urbieta et al. 2011; Rigling et al. 2013). Both mechanisms, land use changes and climate extremes, are at work at the same time (Gimmi et al. 2010), determining feedbacks and interactions difficult to disentangle and providing a challenge for forecasting future vegetation patterns.

Recession of Scots pine forests in southern European landscapes would affect the provision of important ecosystem services, such as protection from hydrogeological hazards, plant and animal diversity, timber, and recreation. A shift from Scots pine to oak can also be problematic because of the loss of useful life traits, as the ability to rapidly colonize open or disturbed ground (Vacchiano et al. 2013). Predictions of future vegetation changes and knowledge of the suitability of pine vs. oak to expected environmental conditions will help managers in developing adaptation strategies to sustain the fulfillment of the desired forest functions (Chmura et al. 2011).

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

2. Methods

Study species

Scots pine is the most widespread coniferous species in Europe, and the most widespread pine in the world (Mirov 1967). Scots pine is a species of continental climates, able to grow in areas with annual precipitation ranging from 200 to 1800 mm (Burns and Honkala 1990). The upper/northern and lower/southern limits of the species correspond with isotherms -1 °C (mean temperature of the coldest month) and +33 °C (mean temperature of the warmest month) respectively (Dahl 1998), even if pine can tolerate more extreme temperatures without tissue damage, especially at the cold end (-90 °C: 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), 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 broadleaved-coniferous forest. However in the drier, central alpine sectors (<700 mm year-1 rainfall) Scots pine often forms stable communities due to limited competiveness 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. 2013, 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. 2007) 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.

Study area

The study area covers the Aosta valley region in Northwestern Italy (3262 km^2) (Figure 1). Topography is shaped by a main east–west oriented valley with several north–south protrusions. Mean annual temperature in Aosta (45°26' N, 7°11' E, 583 m a.s.l.) is 10.9 °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°C. Mean annual rainfall in Aosta amounts to very low values in comparison 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) extending 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 colluvial origin. Soils belong to the series of western and central Alpine soil on igneous and metamorphic rocks (Costantini et al. 2004) and are mostly represented by shallow soils (Lithic, Umbric and Dystric Leptosols), eroded soils (Eutric and Calcaric Regosols), acid soils with organic matter, iron oxides and aluminum accumulation (Dystric Cambisols, Haplic Podzols, Humic Umbrisols), or alluvial soils (Eutric Fluvisols).

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

Downy oak stands covers 3468 ha in the study area (Gasparini and Tabacchi 2011), at elevations of 300–1200 m (but up to 1500 m on rocky outcrops, and 1800 m for isolated individuals), predominantly on shallow soils and carbonatic substrates. Xerophilous stands on south-facing slopes are sparse and slow-growing (1000 TPHA, BA 20 m^2 ha^{-1}), with young individuals often developed from former coppices, grazed woodland, or after invasion on abandoned fallow lands (QMD 10–25 cm, mean height 5–10 m) (Gasparini and Tabacchi 2011). Just as in Scots pine, meso-xerophilous stands on north-facing slopes exhibited higher growth (mean height: 10–15 m) and a mixture degree. Scots pine and downy oak can replace each other in the course of forest dynamics, e.g., by regeneration of pine in sparse and degraded oak woodlands, or the succession of closed-canopy, or declining, pine forests to more tolerant oak (Zavala and Zea 2004).

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 presence/absence of pine and oak in areas with forest cover, since the model could be calibrated against current vegetation conditions only. Rasterization of vector layers and raster resampling were carried out by aggregating to cell means if raster grain was finer than 1 km, and by bilinear (for continuous layers) or nearest neighbor interpolation (for categorical layers) if grain exceeded 1 km (Figure S1). Explanatory variables included the following:

(1) elevation, slope, aspect, southness (i.e., a linearization of aspect: Chang et al. 2004), and topographic position index (TPI: Guisan et al. 1999) computed from a 10 m digital terrain model. A higher TPI is indicative of ridges or hilltops;

(2) climate means (years 1961-1990) at a 1 km resolution, extracted from the Worldclim database (Hijmans et al. 2005). These included mean, minimum, and maximum yearly temperatures (TMIN, TMEAN, TMAX), yearly precipitation (P), precipitation cumulated in the growing season (April-September, GSP), and yearly solar radiation (RAD). Additionally, using mean, minimum, and maximum monthly temperature grids, we computed growing degree days (GDD; base temperature = 5°C) (Fronzek and Carter 2007), and an aridity index (AI) as the difference between monthly precipitation and potential evapotranspiration (PET). PET for month i was computed as

$$0.0023\ \mathrm{RAD_i}\ (\mathrm{TMEAN_i} + 17.8)\ \frac{(\mathrm{TMAX_i} - \mathrm{TMIN_i})}{2}\ \mathrm{days_i}$$

after Zimmermann et al. (2007);

(3) soil variables at a 1 km resolution, extracted from the European Soil database (European Soil Bureau 1999). We selected variables potentially important for tree establishment and growth, namely: available water capacity of the topsoil (AWC), accumulated soil temperature class (ATC), total organic carbon of the topsoil (OC), base saturation (BS), erodibility (ERO), depth to rock (DR), dominant surface textural class (TEXT), and volume of stones (VS). All variables were coded as dummy values;

(4) natural disturbances, such as landslides or severe soil erosion (source: Corine Land Cover 1990 raster coverage, resolution: 500 m), avalanche tracks, and wildfires > 10 ha for the years 1961–1991(sources: Regione Autonoma Valle d'Aosta, Ufficio Neve e Valanghe; and Regione Autonoma Valle d'Aosta, Corpo Forestale Regionale, Nucleo Antincendo Boschivi);

(5) competition by the pre-existing canopy, assessed by extracting the Normalized Difference Vegetation index (NDVI) from a Landsat 5 Thematic Mapper image (path 195, row 28) taken on June 30th, 1987 (resolution: 30 m). The acquisition period was chosen as to be at the peak at the growing season; the image had 10% cloud cover, but clouds were clustered over high elevation, unforested terrain. The image was first converted to top of the atmosphere radiance using standard equations and calibration parameters obtained from the metadata of each scene (Chander et al. 2009). Then, we computed NDVI using band TM4 (near infrared) and band TM3 (visible red) and used it as a proxy of standing forest biomass (Tucker et al. 1979; Pettorelli et al. 2005). As an additional index of competition by forest vegetation, we used percent tree cover from the recently released Landsat Vegetation Continuous Fields (VCF) dataset (Sexton et al. 2013), at a resolution of 30m, based on a Landsat 5 TM image acquired on July 27th, 2001;

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

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

Model runs under future scenarios

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

(1) Climate means for the 2080 decade were extracted from 30-arcsec gridded simulations by the ECHAM5/MPI-OM model from the Max-Planck Institute for Meteorology, Germany (Raible et al. 2006), under the high emission scenario SRES A1B. Under the assumption of a constant solar radiation, we computed GDD, GSP, PET, and AI from the ECHAM-5 grids. For the 2080 scenario, we did not extrapolate the model to pixels exhibiting AI values exceeding the range of current ones (Elith and Leathwick 2009);

(2) Fire frequency and size are supposedly responsive to climate change (Moriondo et al. 2006). In order to simulate the influence of fire preceding the 2080 decade, we used wildfire polygons for the years 1981–2000, i.e., a period that included several extreme fire seasons resulting in a +39% and +26% increase in the frequency and total area burned, respectively, by large fires (>10 ha) relative to 1961–1980;

(3) We simulated two alternative land-use scenarios: 1) urbanization and land abandonment, i.e., every municipality was assigned a "business as usual" scenario of population change using figures for the period 1951–1991, and 2) maintenance of high land use, i.e., all municipalities were assigned 0% variation in population respective to 1951, thereby assuming a continued presence of man and its activities at all rural settings.

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

Model building

Presence/absence of pine and oak in the years 1992–1994 served as a response variable, which we extracted from a regional forest inventory based on a 500 m regular grid. At every grid node, the species and diameter at breast height (DBH) of each living tree (DBH > 7.5 cm) were measured within a variable-radius circular plot (radius: 8–15 m depending on tree density). Plot coordinates were recorded to the nearest meter. Scots pine and downy oak were labeled as present where at least one tree of each species was recorded, and absent otherwise. We assumed that both pine and oak distribution are in equilibrium with the environment (Rohde 2005). For this reason, and because our aim was to model potential niche, no migration constraints were included in the model.

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

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

We carried out k-fold cross-validation of the model by subdividing the data into a 3:1 proportion ($k = 4$). Model specificity and sensitivity were computed for the selected thresholds; the threshold to convert continuous predictions into binary ones was iteratively chosen to maximize the area under the curve (AUC).

The ensemble prediction was computed from all model realizations with AUC >0.75. The probability of occurrence for the ensemble prediction was the mean of the selected models' predictions, weighted by the model AUC. Model residuals were scrutinized to detect the absence of trends against predicted values and independent variables; a variogram was fitted to assess the degree of residual spatial autocorrelation. Ensemble models were run for the whole study region to obtain a map of potential species distribution under current and future climate, assuming niche conservationism (Wiens et al. 2010). We classified simulated presence/absence of both species using an occurrence probability threshold of 0.6, and assessed projected area changes and elevational shifts in the distribution of pine and oak under the climate change and climate change + intense land use scenarios. All analyses were carried out using the Biomod2 package (Thuiller et al. 2013) for R (R Core Development Team 2013).

Effect of extreme drought events

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

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

3. Results

Scots pines were detected in 460 (27%) out of 1730 inventory plots, and downy oak in 181 (10%). After screening for collinearity, 18 predictors were retained for subsequent analyses (Table 1). Since most climate-related variables were correlated to each other and to elevation, we retained only aridity index (AI) as the main climate predictor; Pearson’s correlation between AI and Worldclim variables was always higher than 0.95 (e.g., $R = -0.995$ vs. mean annual temperature, $R = 0.993$ vs. annual precipitation, $R = -0.962$ vs. GDD).

AI was the most important predictor for the current distribution of both pine and oak (Table 2), with higher occurrence probability at low water balance levels (Figure S2). However, MARS captured a reduced probability of occurrence for Scots pine at very low values of the aridity index (i.e., very dry sites). Beyond aridity, variables associated to high probability of Scots pine occurrence were southness, TPI, population change, building density, and past fires – the last two only in the ANN model. Soil erosion, NDVI, and road density (in the ANN model) decreased the probability of pine presence (Figure S2a). Explanatory variables of oak distribution 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) (Figure 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 versus a current 0.36 across the whole study area) (Figure 3). However, it increased under the intense land use scenario (0.45) (Figure 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 (Figure 5); mean elevation of simulated presence points shifted from 1328 m to 1528 m a.s.l. under climate warming, and to 1473 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, 10100 ha under climate change only, and 14700 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 (Figure 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.

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

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

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

These factors help explain the response of Scots pine distribution in 2080 under the A1B warming scenario, i.e., a modest reduction of habitat suitability, but a significant increase of its optimum elevation. At low elevations, in fact, aridity could reach the lower limits for the species to persist, as suggested by the MARS response curve (Garzon et al. 2008). This change is partially counteracted in a scenario where land 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 (Dirnbock 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 topo-climatic 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, seedling vitality (Eilmann et al. 2006; Poyatos et al. 2008; Moran-Lopez 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. 2009). Ensemble models in Biomod2 are obtained by averaging model prediction and excluding models with low predictive power (AUC <0.75); model predictions are weighted by the AUC of their respective modeling approach. In this study, all three model approaches produced an AUC >0.75. However, differences in importance of explanatory variables and shape of response curves were apparent. MARS are more flexible than GLM as they are fit using piecewise linear splines, and are particularly useful when assuming that the shape of species' responses is not linear (Leathwick et al. 2005). ANN, on the other hand, are not based on specific distribution functions of the response. They are robust to noisy and non-linear responses, and allow for categorical predictors (such as soil characteristics in this study). Therefore, they are particularly appropriate in an exploratory context. On the other hand, they are sensitive to multicollinearity and prone to overfitting, and interpretation of causal relatioships for individual predictors is not straightforward (Manel et al. 1999). The differences are apparent in species response curves (Figure S2), with MARS and ANN capable of detecting non-linear responses to some explanatory variables that were not picked up by GLM, despite a similar predictive performance. This is reflected by the higher importance of some explanatory variables, such as Roads, Buildings, TPI, or Erosion, under models capable of detecting non-linear species responses (Table 2).

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

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

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Tables

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

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). Codes for explanatory variables are given in Table 1.

	Scots pine			**Downy oak**		
Variable	**GLM**	**MARS**	**ANN**	**GLM**	**MARS**	**ANN**
AI	0.650	0.645	0.733	0.848	0.830	1.000
Slope	0.000	0.086	0.006	0.038	0.087	0.023
TPI	0.145	0.162	0.000	0.099	0.103	0.000
Southness	0.180	0.393	0.283	0.210	0.269	0.220
ATC	0.000	0.017	0.000	0.078	0.042	0.000
AWC	0.000	0.000	0.000	0.000	0.000	0.000
DR	0.000	0.000	0.000	0.251	0.138	0.000
ERO	0.000	0.000	0.000	0.000	0.000	0.000
OC	0.000	0.000	0.000	0.044	0.000	0.000
VS	0.000	0.000	0.000	0.160	0.000	0.000
Avalanches	0.000	0.000	0.000	0.000	0.000	0.000
Wildfires	0.010	0.000	0.000	0.000	0.000	0.000
Erosion	0.000	0.061	0.319	0.011	0.028	0.109
Depop	0.069	0.029	0.000	0.027	0.041	0.000
Roads	0.000	0.000	0.459	0.016	0.029	0.159
Buildings	0.000	0.017	0.367	0.027	0.155	0.201
VCF	0.000	0.028	0.018	0.000	0.024	0.023
NDVI	0.134	0.093	0.000	0.006	0.074	0.000

Captions of figures

Fig. 1 – Location of the study region and area covered by forests (in green).

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.

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).

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).

Supplementary material

Fig. S1 – Explanatory variables used in this study. Codes for explanatory variables are in Table 1

Fig. S2 – Response curves for SDM of (a) Scots pine, and (b) downy oak in current conditions. Models: GLM (solid line), MARS (dashed), ANN (dotted). Codes for explanatory variables are in Table 1.

tables
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code	description	range	mean
bio01	Mean annual temperature[a]	-0.6 – 11.1	4.9
bio05	Max temperature of warmest month[a]	10.8 – 26.7	18.5
bio06	Min temperature of coldest month[a]	-10.8 – -2.9	-6.9
bio07	Temperature annual range[a]	21.3 – 29.6	25.4
bio10	Mean temperature of warmest quarter[a]	6.4 – 20	12.8
bio11	Mean temperature of coldest quarter[a]	-7.2 – 2	-2.8
bio12	Annual precipitation[a]	796 – 1828	1263.3
bio18	Precipitation of warmest quarter[a]	225 – 465	335.6
GDD	Growing degree days above 5 °C	257 – 2656	1181.2
GSP	Precipitation april-september	437 – 913	663.5
AI	Aridity index (bio12 -PET)	-638 – 1252	311.0
DTM	Elevation[b]	308 – 2493	1514.3
slope	Slope from DTM	0 – 44	17.0
TPI	Topographic Position Index	-3.0 – 3.1	-0.4
southness	Linearization of aspect	0 – 180	97.2
ATC	Soil accumulated temperature class[c]	1 – 3	-
AWC	Available water capacity in the topsoil[c]	1 – 3	-
BS	Soil base saturation[c]	1 – 2	-
DR	Soil depth to rock[c]	1 – 4	-
ERO	Soil erodibility[c]	3 – 5	-
OC	Organic carbon in the topsoil[c]	1 – 3	-
TEXT	Soil texture (from coarse to fine)[c]	0 – 2	-
VS	Volume of stones in the soil[c]	0 – 2	-
Avalanches	Number of avalanche polygons[b]	0 – 3	0.1
Wildfires	Number of fire polygons, 1961-1990[b]	0 – 3	0.0
Erosion	Total area subject to landslide or erosion[d]	0 – 14523	656.9
Depop	Change in population 1951-1991[e]	-59 – 135	2.1
Roads	Total road length[b]	0 – 8485	1812.0
Buildings	Total buildings area[b]	0 – 40190	1591.8
VCF	Tree cover from Landsat (2001)[f]	0 – 99	29.9
NDVI	NDVI from Landsat (1987)	0.20 – 0.66	0.30

Bold: Explanatory variables in species distribution models

Data sources: [a] Hijmans et al. (2005); [b] Regione Autonoma Valle d'Aosta; [c] European Soil B

units	resolution
°C	30 arcsec
°C	30 arcsec
°C	30 arcsec
°C	30 arcsec
°C	30 arcsec
°C	30 arcsec
mm	30 arcsec
mm	30 arcsec
°C	30 arcsec
mm	30 arcsec
mm	30 arcsec
m asl	10 m
°	10 m
-	10 m
°	10 m
dummy	1 km
dummy	1 km
dummy	1 km
dummy	1 km
dummy	1 km
dummy	1 km
dummy	1 km
dummy	1 km
count	10 m
count	10 m
m^2	500 m
% change	municipality
m	500 m
m^2	500 m
%	30 m
0-1	30 m

ureau (1999); [d] European Environment Agency (2013); [e] ISTAT (2012); [f] Sexton et al. (2013)

	Scots pine			Downy oak		
Variable	**GLM**	**MARS**	**ANN**	**GLM**	**MARS**	**ANN**
AI	0.650	0.645	0.733	0.848	0.830	1.000
Slope	0.000	0.086	0.006	0.038	0.087	0.023
TPI	0.145	0.162	0.000	0.099	0.103	0.000
Southness	0.180	0.393	0.283	0.210	0.269	0.220
ATC	0.000	0.017	0.000	0.078	0.042	0.000
AWC	0.000	0.000	0.000	0.000	0.000	0.000
DR	0.000	0.000	0.000	0.251	0.138	0.000
ERO	0.000	0.000	0.000	0.000	0.000	0.000
OC	0.000	0.000	0.000	0.044	0.000	0.000
VS	0.000	0.000	0.000	0.160	0.000	0.000
Avalanches	0.000	0.000	0.000	0.000	0.000	0.000
Wildfires	0.010	0.000	0.000	0.000	0.000	0.000
Erosion	0.000	0.061	0.319	0.011	0.028	0.109
Depop	0.069	0.029	0.000	0.027	0.041	0.000
Roads	0.000	0.000	0.459	0.016	0.029	0.159
Buildings	0.000	0.017	0.367	0.027	0.155	0.201
VCF	0.000	0.028	0.018	0.000	0.024	0.023
NDVI	0.134	0.093	0.000	0.006	0.074	0.000

figure S2a

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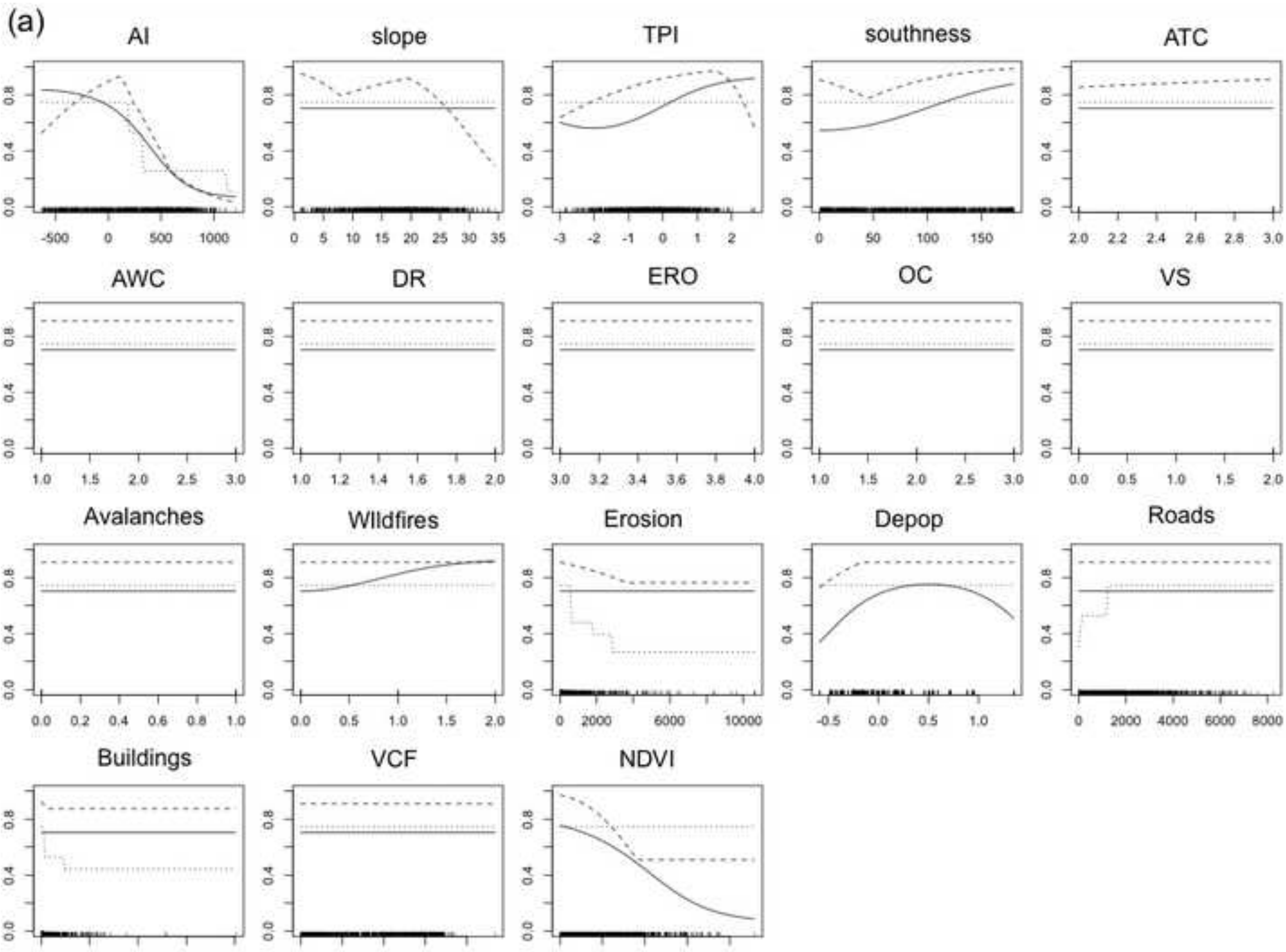

figure S2b
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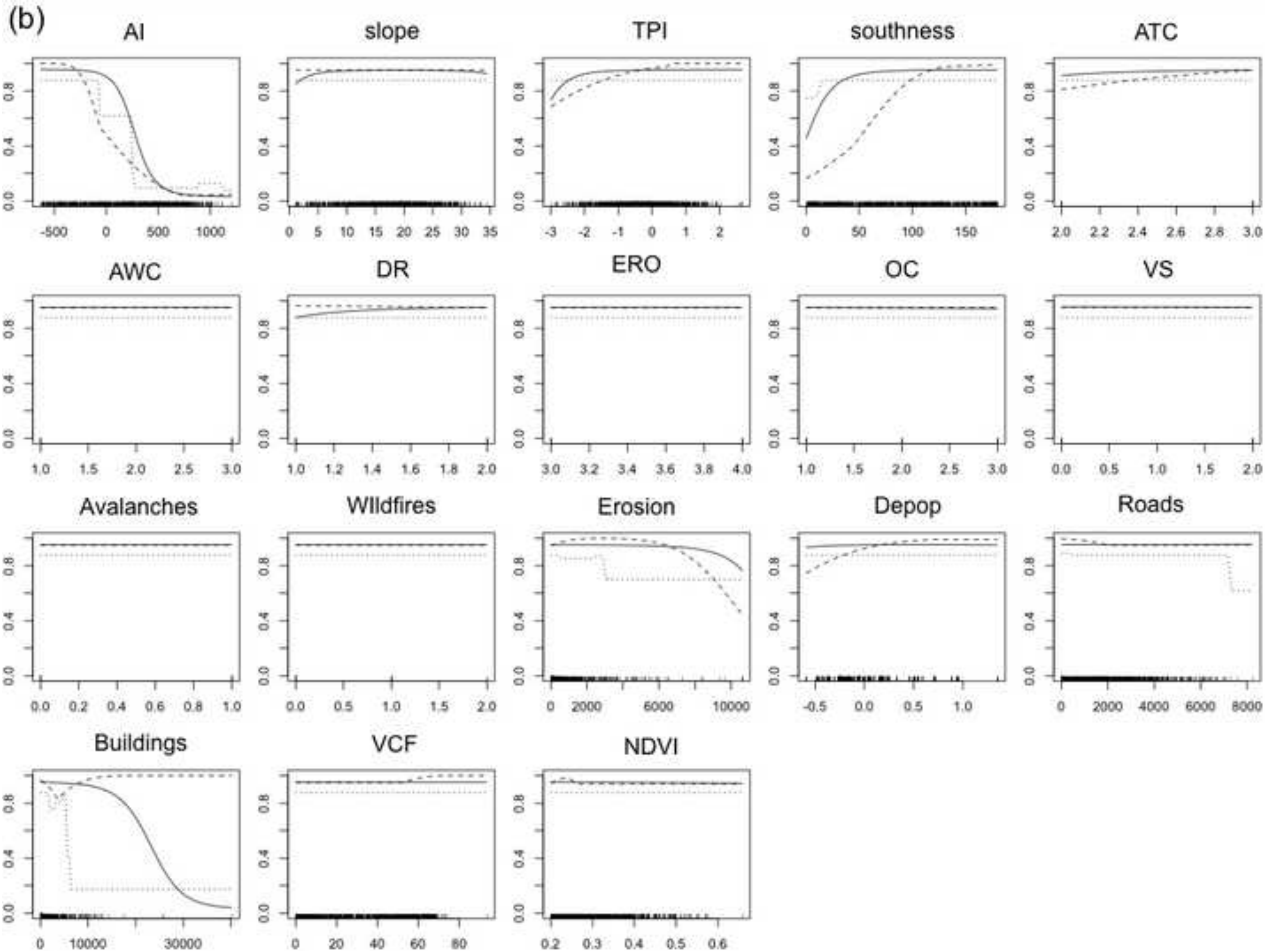

figure 5a
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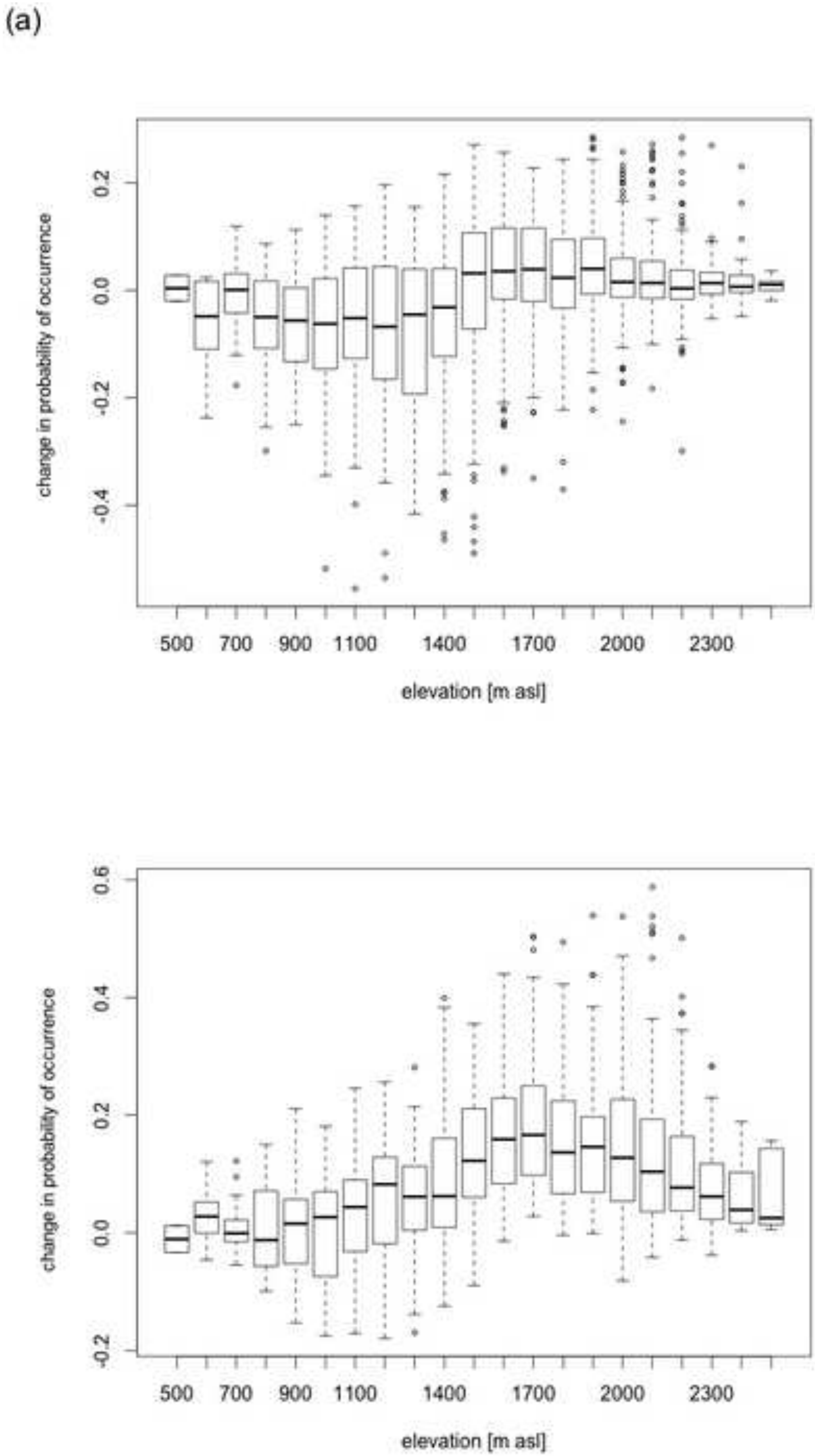

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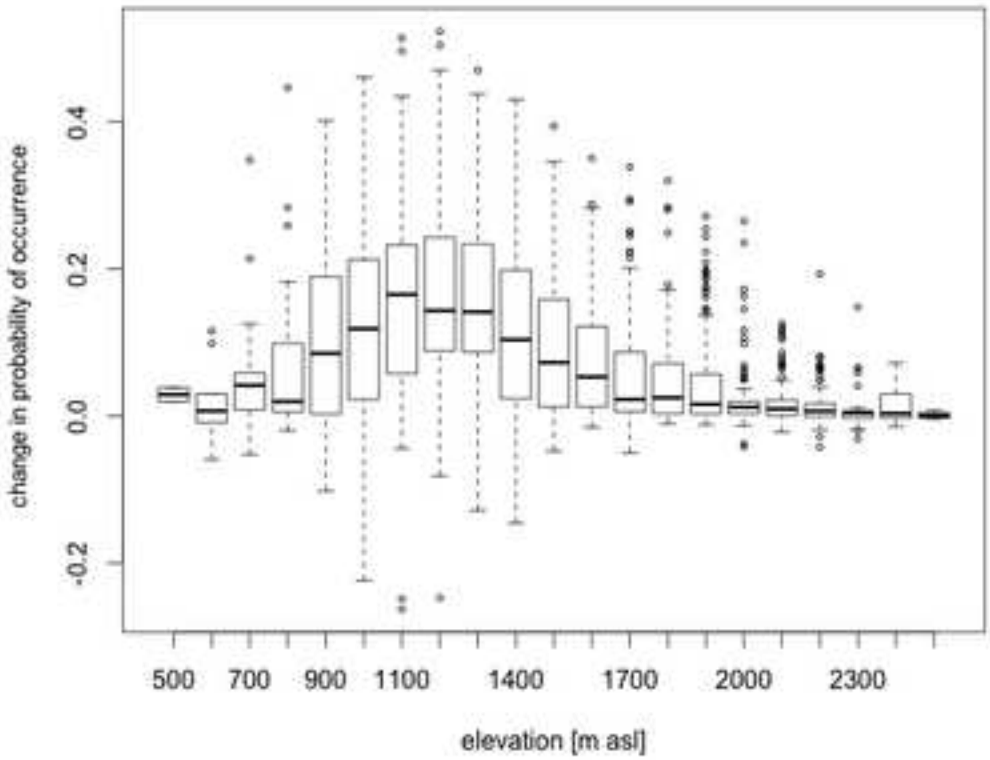
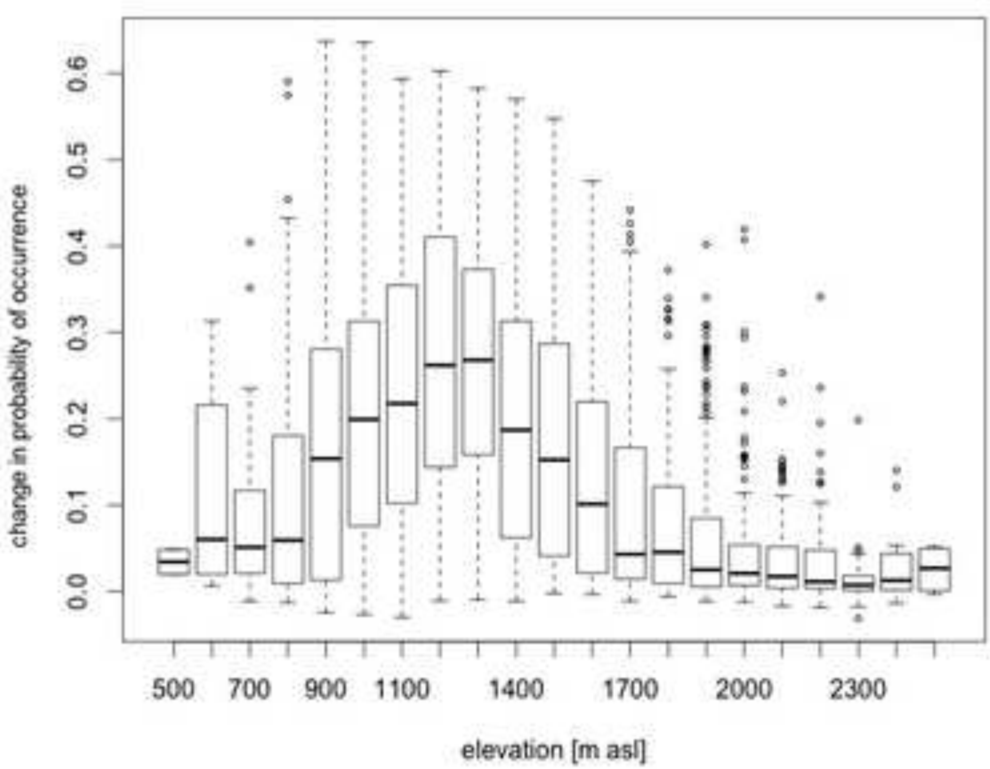
(b)





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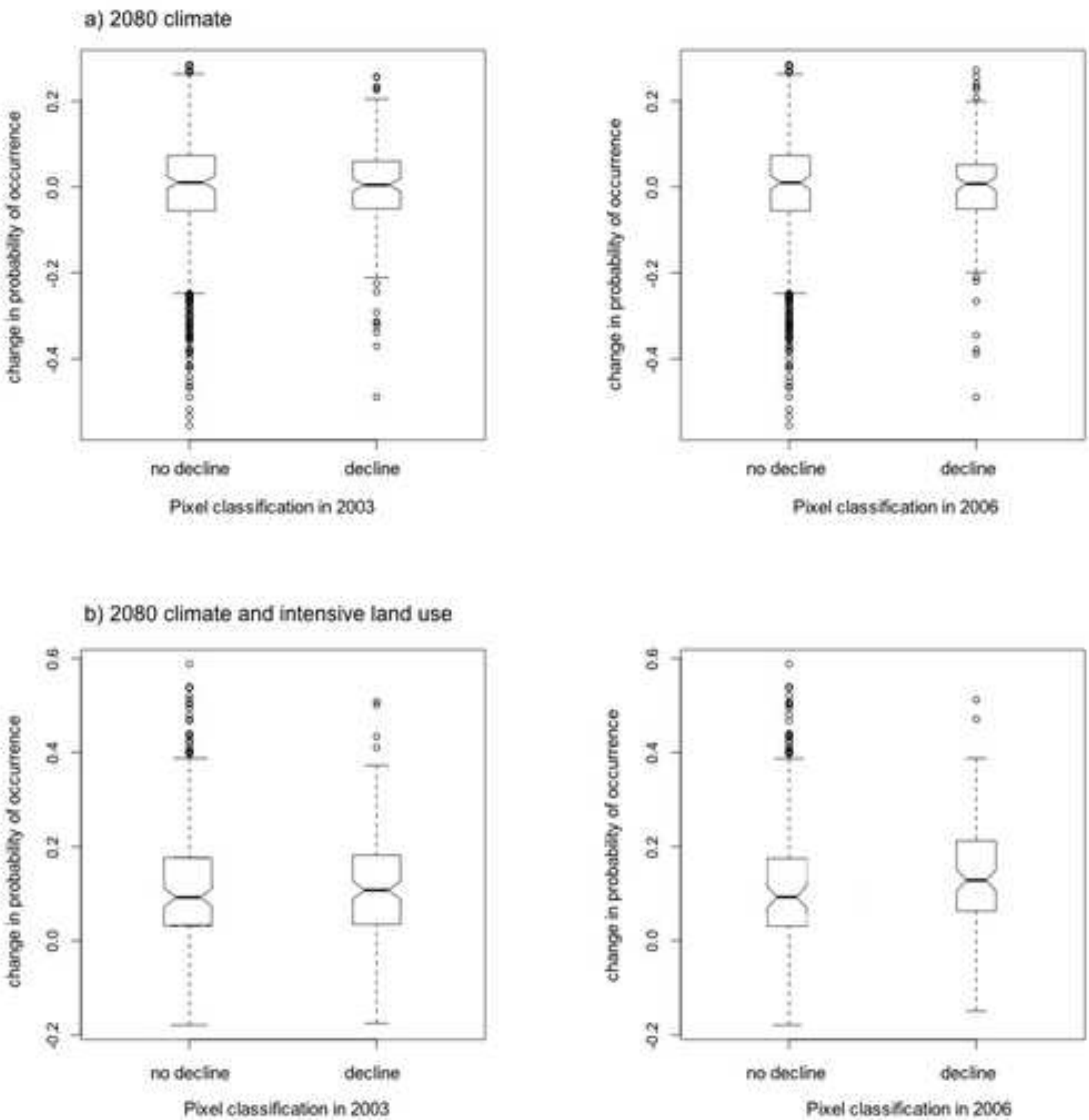

figure 1
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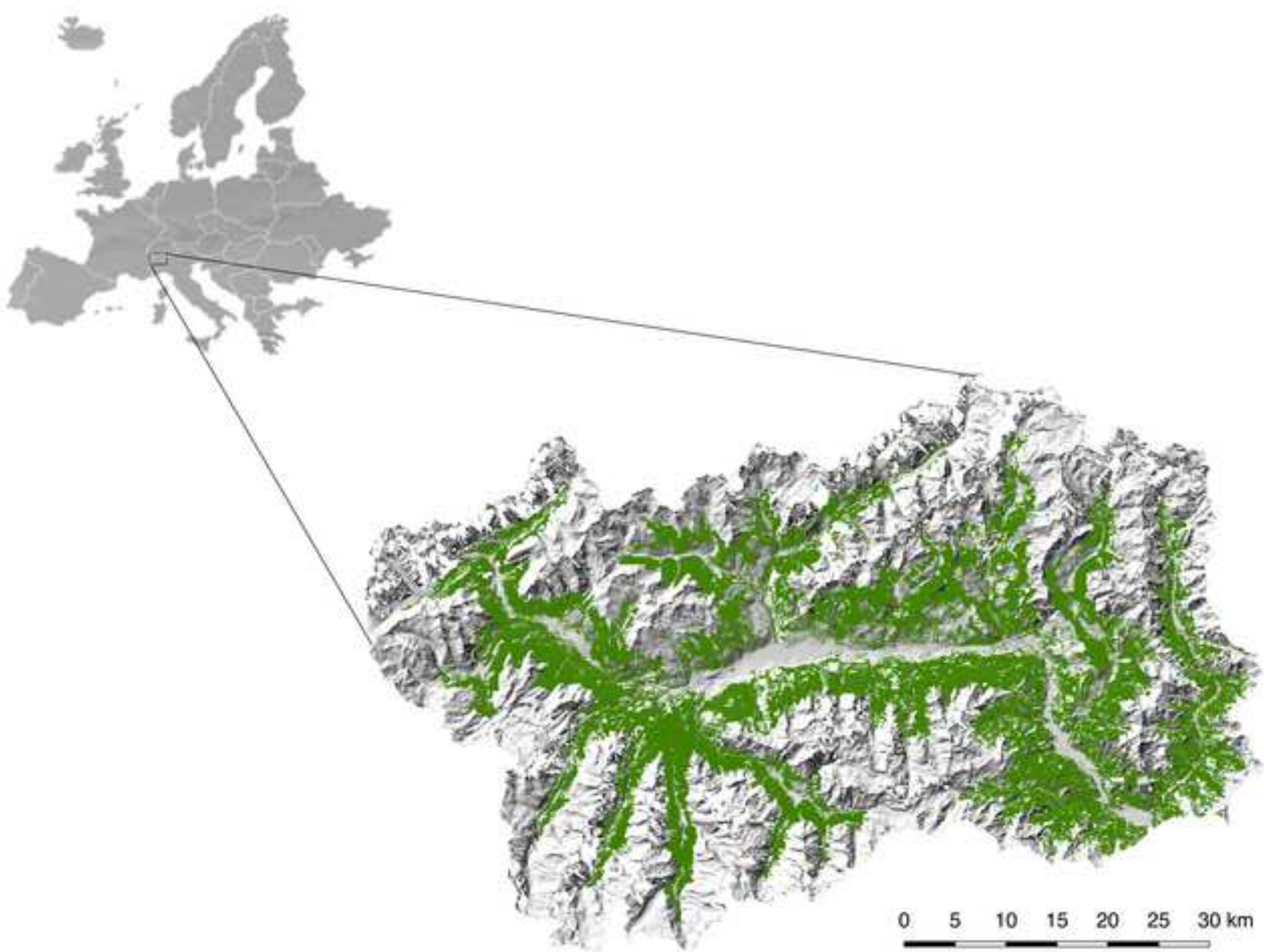

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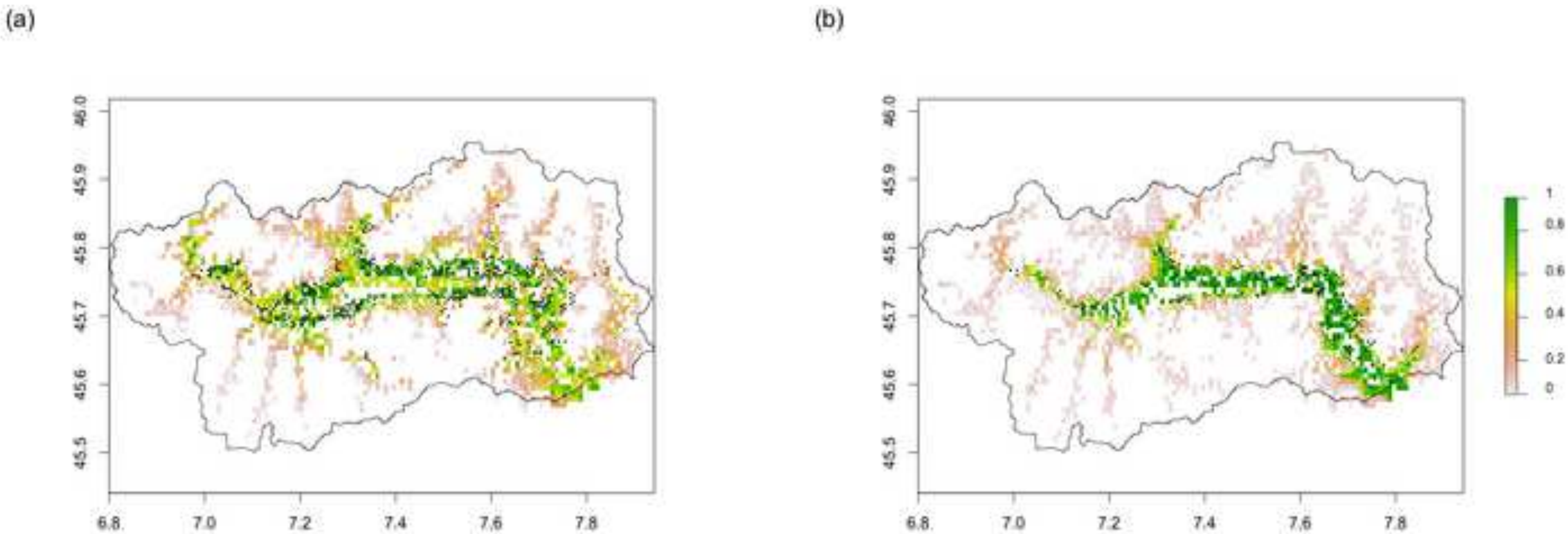

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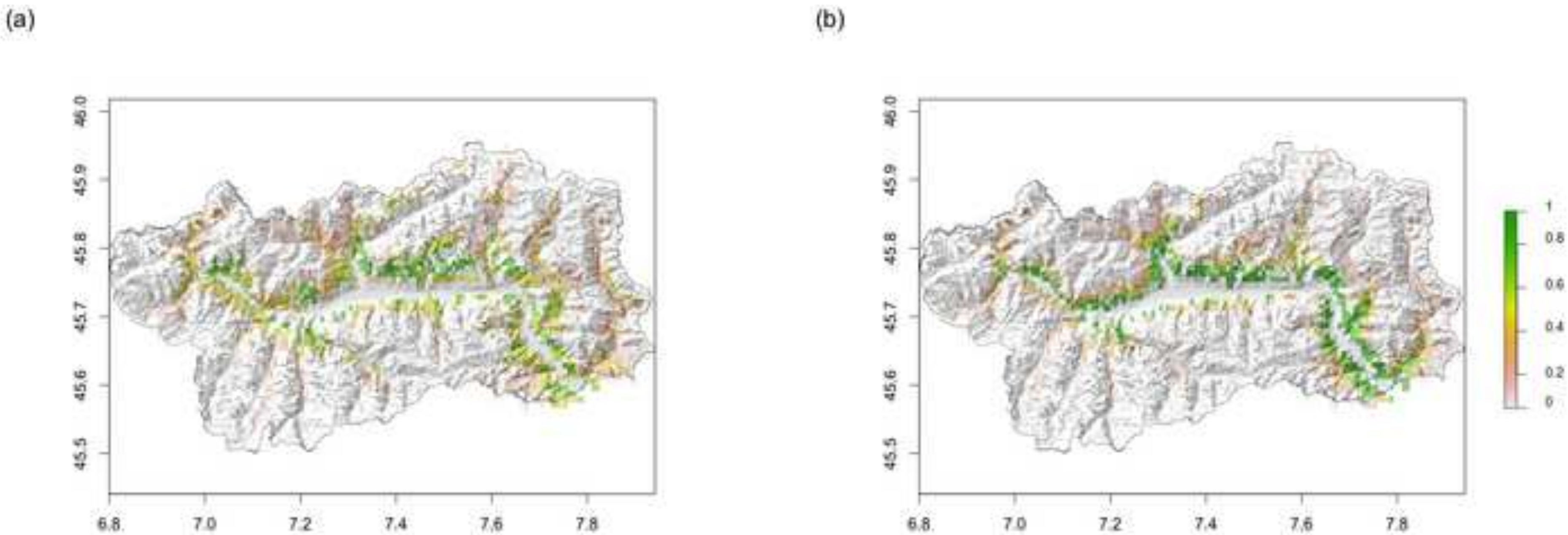

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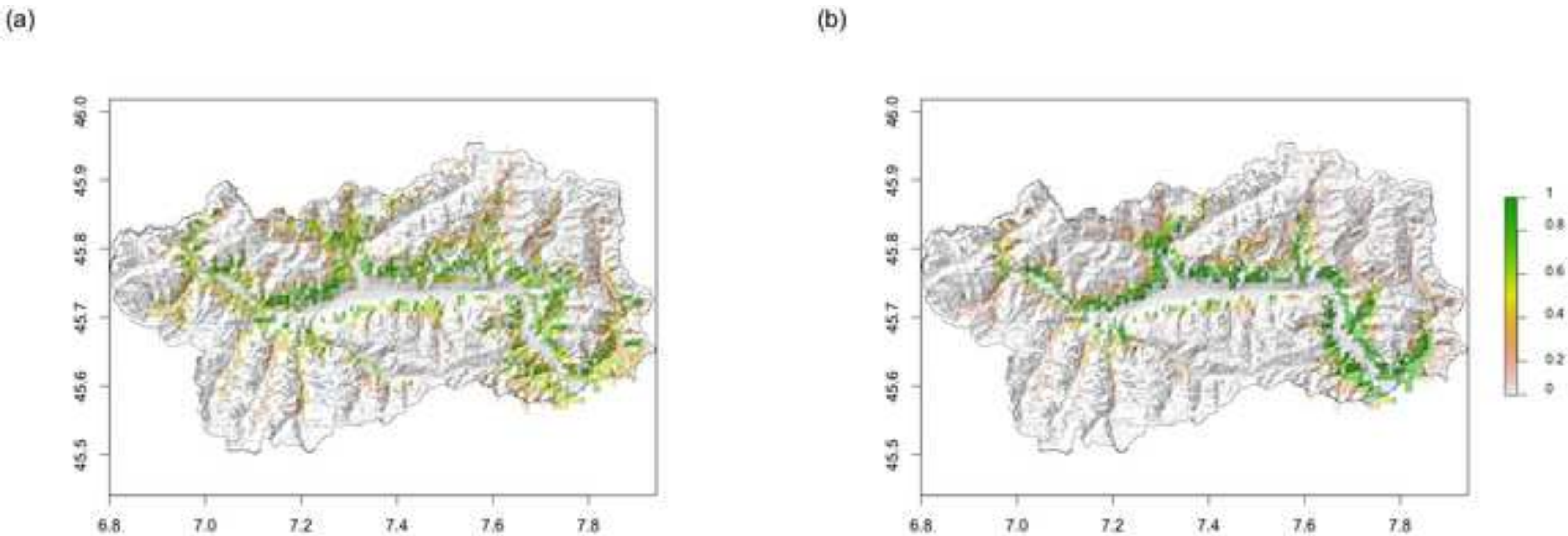

figure S1

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