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Climate regulation ecosystem services and biodiversity
conservation are enhanced differently by climate- and fire-smart
landscape managementJoão C Campos^{1,2,*} , Sara Rodrigues^{1,2} , Ângelo Sil^{1,2,3,4} , Virgílio Hermoso⁵ , Teresa R Freitas³ ,
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E-mail: jc_campos@cibio.up.pt**Keywords:** carbon sequestration, climate change, ecosystem services, landscape planning, land-use change, mountain rural areasSupplementary material for this article is available [online](#)

Abstract

The implementation of climate-smart policies to enhance carbon sequestration and reduce emissions is being encouraged worldwide to fight climate change. Afforestation practices and rewilding initiatives are climate-smart examples suggested to tackle these issues. In contrast, fire-smart approaches, by stimulating traditional farmland activities or agroforestry practices, could also assist climate regulation while protecting biodiversity. However, there is scarce information concerning the potential impacts of these alternative land management strategies on climate regulation ecosystem services and biodiversity conservation. As such, this work simulates future effects of different land management strategies in the Transboundary Biosphere Reserve of Meseta Ibérica (Portugal-Spain). Climate-smart ('Afforestation', 'Rewilding') and fire-smart ('Farmland recovery', 'Agroforestry recovery') scenarios were modelled over a period of 60 years (1990–2050), and their impacts on climate regulation services were evaluated. Species distribution models for 207 vertebrates were built and future gains/losses in climate-habitat suitability were quantified. Results suggest climate-smart policies as the best for climate regulation (0.98 Mg C ha⁻¹ yr⁻¹ of mean carbon sequestration increase and 6801.5 M€ of avoided economic losses in 2020–2050 under Afforestation scenarios), while providing the largest habitat gains for threatened species (around 50% for endangered and critically endangered species under Rewilding scenarios). Fire-smart scenarios also benefit carbon regulation services (0.82 Mg C ha⁻¹ yr⁻¹ of mean carbon sequestration increase and 3476.3 M€ of avoided economic losses in 2020–2050 under Agroforestry scenarios), benefiting the majority of open-habitat species. This study highlights the main challenges concerning management policies in European rural mountains, while informing decision-makers regarding landscape planning under global change.

1. Introduction

Global temperature and precipitation have been shifting due to increased climate change effects (Sippel *et al* 2020), ultimately contributing to disruption of entire ecosystems worldwide (Turner *et al* 2020). The severe implications of climate change to the biosphere and human well-being has led to collective global efforts to develop policy actions that may counteract these effects (e.g. formulation of the Paris Agreement). Specifically, establishing and reinforcing sustainable low carbon development strategies have been encouraged, through actions focused on decreasing anthropogenic carbon dioxide (CO₂) emissions and on maintaining and expanding the capacity of natural carbon sinks (Rockström *et al* 2017). The maintenance of climate regulation ecosystem services (CRES) stands out as a crucial measure to fight climate change, but the supply of these services is strongly influenced by changes in land use and land cover (LULC). In fact, around 30% of the global carbon emissions are caused by LULC change, especially by deforestation and agricultural practices (Scherr *et al* 2012). For these reasons, researchers have sought land management solutions capable of supplying enhanced climate regulation services, generally referred to as ‘climate-smart’ landscape management.

The concept of climate-smart management was first applied in agricultural systems as an approach to effectively support local development and food security in a changing climate (FAO 2010, Scherr *et al* 2012, Lipper *et al* 2014). Climate-smart was later extrapolated to forest management (see Nabuurs *et al* 2018), being currently defined as adaptive forest management solutions to sustain ecosystem integrity, functions, goods and services, while minimizing the impact of climate-induced changes on forests and on human well-being (see Bowditch *et al* 2020). Global initiatives have been planned to develop climate-smart landscapes, which are particularly focused on the restoration of degraded forests and afforestation actions, i.e. the (re)creation of new forest areas (e.g. through tree planting) not naturally forested in recent times (Di Sacco *et al* 2021). For instance, the World Economic Forum prompted a cross-corporate alliance to support the UN Decade on Ecosystem Restoration 2021–2030 through the plantation of three trillion trees (www.1t.org/). Climate-smart strategies are also being encouraged in Europe, with the European Commission establishing the plantation of three billion trees across the European Union (EU) until 2030 as a key commitment of its recently adopted Biodiversity Strategy for 2030 (European Commission 2020). Some studies have highlighted large benefits of climate-smart initiatives in European landscapes (Nabuurs *et al* 2018, Bowditch *et al* 2020, Verkerk *et al* 2020), indicating potential mitigation impacts of carbon emissions in the EU of approximately 441 Mt CO₂ per year by 2050 (Nabuurs *et al* 2017). However,

large-scale tree-planting initiatives have also been criticized by the scientific community due to consequent detrimental ecological and economic impacts (e.g. Bond *et al* 2019, Holl and Brancalion 2020, Selva *et al* 2020) as well as a potential increased wildfire risk (Hermoso *et al* 2021). Objectors argue that not only do these actions have limited efficacy in regulating climate change, but might also restrain key opportunities to reduce fossil fuel emissions (Anderegg *et al* 2020), to decrease deforestation trends and to restore degraded forests through natural regeneration processes (Bond *et al* 2019, Gómez-González *et al* 2020). Furthermore, these strategies might compromise important habitats for biodiversity conservation that also constitute efficient carbon sinks, such as perennial grasslands, peatlands and wetlands (Bond *et al* 2019).

In this context, the current land abandonment trends of European landscapes (see Lasanta *et al* 2017), might facilitate, or propel, the establishment of passive climate-smart strategies, particularly focused on natural habitat recovery with reduced human intervention to restore ecosystem processes, a management approach commonly coined as ‘rewilding’ (see Gillson *et al* 2011). Former studies indicate that approximately 150 000 km² of farmland areas could be abandoned in the EU by 2030 (Nabuurs *et al* 2017), mainly due to political, social, economic, and environmental drivers that lead to high migration rates to urban areas and consequent local population ageing (Leal Filho *et al* 2017). For these reasons, these tendencies might be an opportunity to implement rewilding approaches to improve nature conservation and enrich areas no longer viable from a socio-economic point of view (Queiroz *et al* 2014), while boosting both biodiversity conservation and ecosystem services. In fact, by improving climate regulation services (Strassburg *et al* 2020), and favouring several biological communities, such as forest-dwelling birds (Regos *et al* 2016), large mammals (Navarro and Pereira 2012), and endemic species of conservation concern (Campos *et al* 2021a), rewilding approaches might correspond to one of the most advantageous climate-smart strategies that could be straightforwardly explored in many European landscapes.

Nonetheless, the application of climate-smart solutions, motivated by either afforestation actions or rewilding initiatives, can also threaten species adapted to early successional habitats, due to vegetation encroachment (e.g. shrublands) and forest expansion (Regos *et al* 2016). Additionally, the development of densely vegetated areas might increase wildfire hazard and severity, fed by the higher availability and connectivity of accumulated fuel (Moreira *et al* 2011). These impacts might be particularly severe in areas where fire represents a primary disturbance component, such as in the Mediterranean regions of Southern Europe (Dupuy *et al* 2020, McLauchlan *et al* 2020). Indeed, these regions are suffering from large

and severe fires responsible for economic, social and environmental damages (Turco *et al* 2018, Sil *et al* 2019), mainly due to strong climatic seasonality and irregularity, and warm-dry summers magnified by climate change and rural abandonment (Moreira *et al* 2011). Climate-smart policies inducing afforestation and rewilding actions in the already abandoned and densely vegetated rural areas of Southern Europe may exacerbate the already harsh impacts of extreme wild-fires (Hermoso *et al* 2021).

In this regard, researchers have emphasized the need for sustainable landscape strategies to control and mitigate fire ignitions and spread (Moreira *et al* 2020). ‘Fire-smart’ landscape management represents one of these strategies, focusing on fuel-reduction and fuel-conversion treatments through the promotion of less flammable and more fire-resilient land cover types and higher landscape diversity (see Fernandes 2013). This management strategy is already considered by the European Commission as an essential solution to address forest fires (Tedim *et al* 2016), having also the potential to assist biodiversity conservation and to boost ecosystem services, such as carbon storage and sequestration (Pais *et al* 2020). A fire-smart landscape can be supported through sustainable agroforestry planning and management, by integrating fire-resilient and fire-resistant LULC systems with previously abandoned or active agricultural areas. Alternatively, researchers have suggested that the return of traditional farming activities supported by the EU Common Agricultural Policy, might allow sustaining biological communities adapted to human-mediated habitats (Moreira *et al* 2020, Pais *et al* 2020, Campos *et al* 2021a), while decreasing fire risks by controlling fuel accumulation on the landscape and generating open areas that provide opportunities for fire control (Moreira and Pe’er 2018, Aquilué *et al* 2020, Lomba *et al* 2020). Therefore, re-establishing and developing farming and agroforestry activities could potentiate the implementation of fire-smart solutions, especially where afforestation and rewilding might be counterproductive for local fire mitigation and biodiversity conservation.

Notwithstanding, few studies have thoroughly assessed the potential effects of alternative land management strategies on ecosystem services (e.g. CRES), their economic valuation, and how they might affect local biodiversity communities. These assessments become paramount to successfully implement appropriate landscape policies in regions that are subjected to growing environmental and ecological change. As such, we explore in this study the impact of two climate-smart (‘Afforestation’ and ‘Rewilding’) and two fire-smart (‘Farmland recovery’ and ‘Agroforestry recovery’) management strategies on CRES and on biodiversity conservation. Specifically, we aim to assess how different land management scenarios based on ongoing European Commission policies could contribute to future CRES supply

and societal benefits (i.e. economic damages avoided due to carbon emissions reduction), and how they could affect biodiversity in a Southern European rural mountainous region affected by abandonment under future climate change scenarios.

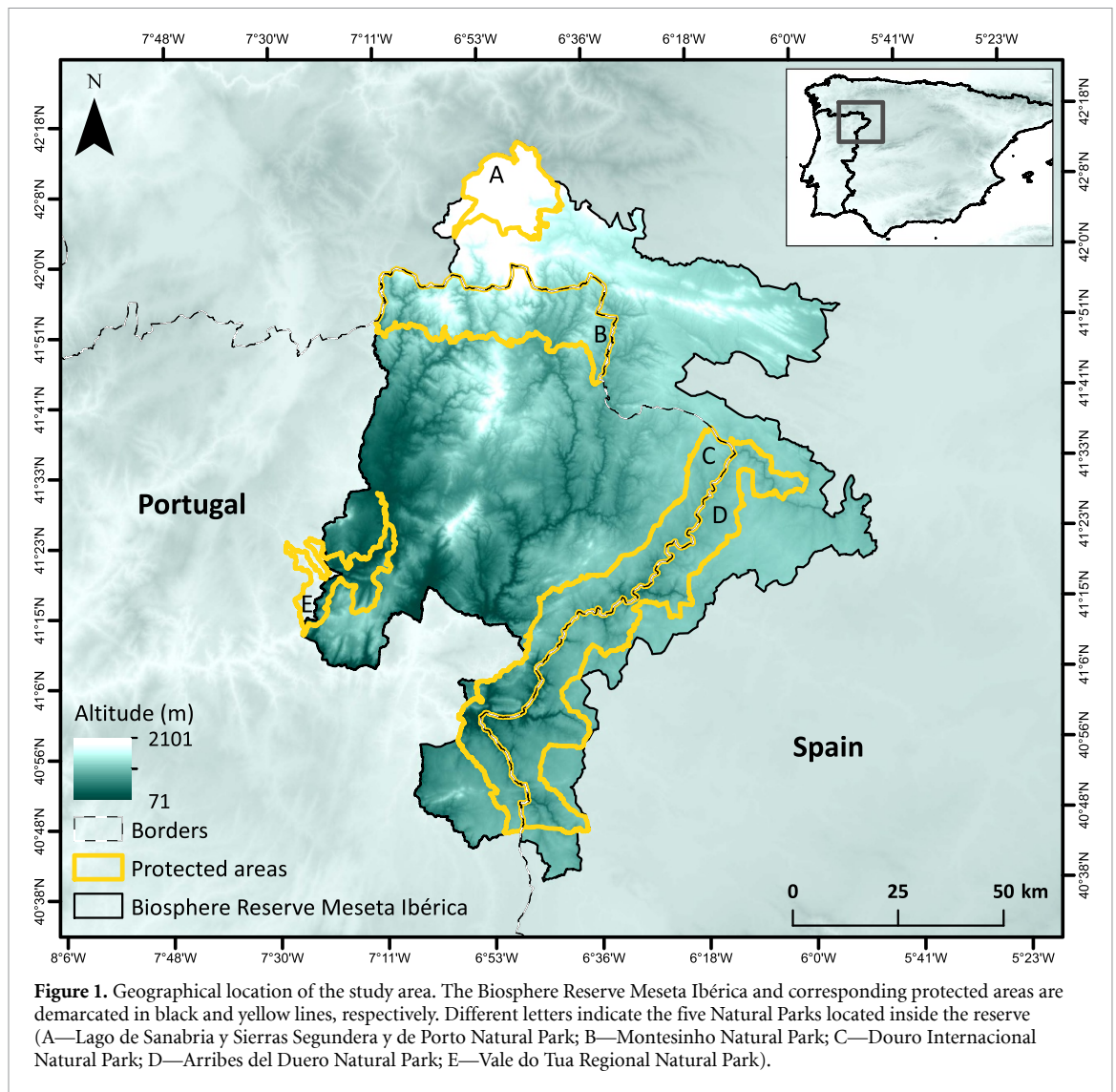
2. Methods

2.1. Study area

The Transboundary Biosphere Reserve of Meseta Iberica is located in the NW of the Iberian Peninsula, including the Bragança district, in Portugal, and the Salamanca and Zamora provinces in Spain. The reserve occupies a surface area of 11 326 km², and it is characterized by a large altitudinal range (from 71 to 2101 m; figure 1). The climate is predominantly Mediterranean, characterized by dry-warm summers (July–September) and cool-wet winters (January–March; Deitch *et al* 2017). Mean annual total precipitation varies annually from 200–300 to more than 1200 mm (Deitch *et al* 2017, Santos and Belo-Pereira 2022).

The area is markedly agricultural, but comprises extensive dry heathland (dominated by *Erica*, *Pteropartum*, *Cystisus*, and *Cistus* species) and agro-pastoral areas and substantial forest areas, which translates into heterogeneous landscapes with high natural and heritage values. The most common forests are dominated by maritime pine (*Pinus pinaster*), Pyrenean oak (*Quercus pyrenaica*), and holm oak (*Quercus ilex*). Chestnut orchards (*Castanea sativa*) are the most common agroforestry system.

In the last 30 years, agricultural and forest areas have declined in the reserve, mainly associated with socio-economic drivers, such as population ageing and rural depopulation. For instance, the population density of Trás-os-Montes e Alto Douro in Portugal and the rural regions of Zamora in Spain decreased from approximately 13 to 9 inhabitants km⁻² between 1981 and 2020 (www.pordata.pt) and from 13 to 10 inhabitants km⁻² between 1996 and 2020 (www.ine.es), respectively. These two provinces encompass the majority of the study area, representing the contemporary tendencies of population decline in the reserve (currently, with 14 inhabitants km⁻²). In fact, the decline in population density is probably higher in rural areas (that compose most of the reserve), since the movement of population from rural areas towards medium size cities within these two regions are not captured by regional level statistics. These drivers have led to land abandonment and consequent land-use conversions that gradually shaped the landscape over time, mostly associated with increases in shrublands in detriment of agricultural areas (Sil *et al* 2019). The landscape changes potentially modified biodiversity patterns and, presumably, local fire regimes. Contemporary trends in burned area, either positive or negative,



vary within the area as an outcome of the opposing effects of LULC changes and increasingly stronger fire suppression (e.g. decrease in burned area; Silva *et al* 2019, but see also Turco *et al* 2016).

The biodiversity conservation of the reserve is of paramount importance at the European level, since it encompasses five protected natural parks (which occupy almost 30% of the entire reserve) and 24 Natura 2000 sites (figure 1). The area is characterized by high levels of species diversity, counting around 250 species of vertebrates, including several Iberian endemics and emblematic species of conservation concern, such as the Egyptian vulture (*Neophron percnopterus*), the Iberian wolf (*Canis lupus signatus*), the Seoane's viper (*Vipera seoanei*), and the Iberian frog (*Rana iberica*).

2.2. Landscape spatial data and scenarios

The spatial land cover dataset of the reserve used in modelling and simulation in this study consisted of six raster files (100 m resolution). Land cover information for dates in the past was retrieved from the

CORINE Land Cover database for 1990 and 2018 (<https://land.copernicus.eu/pan-european/corine-land-cover>), and reclassified into ten main land cover classes: urban, agro-pastoral (i.e. croplands), agroforestry, grasslands, shrublands, forest (deciduous, conifers and mixed), water and others (see appendix A for details available online at stacks.iop.org/ERL/17/054014/mmedia). Land cover information for 2050 consisted of four alternative landscape scenarios (ten replicates per scenario) under two main landscape storylines: climate-smart and fire-smart policies (see figure 2 and table 1). The future scenarios in the reserve were built by applying the *Scenario Generator* module of the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) model, a tool designed to quantify, evaluate and map the effect of LULC on several ecosystem services (Sharp *et al* 2018; see figure 2 and appendix B for details). Despite the availability of several ecosystem service tools, such as the ARIES (Artificial Intelligence for Ecosystem Services; Villa *et al* 2009), the i-Tree (www.itreetools.org/), and the SolVES (Social Values

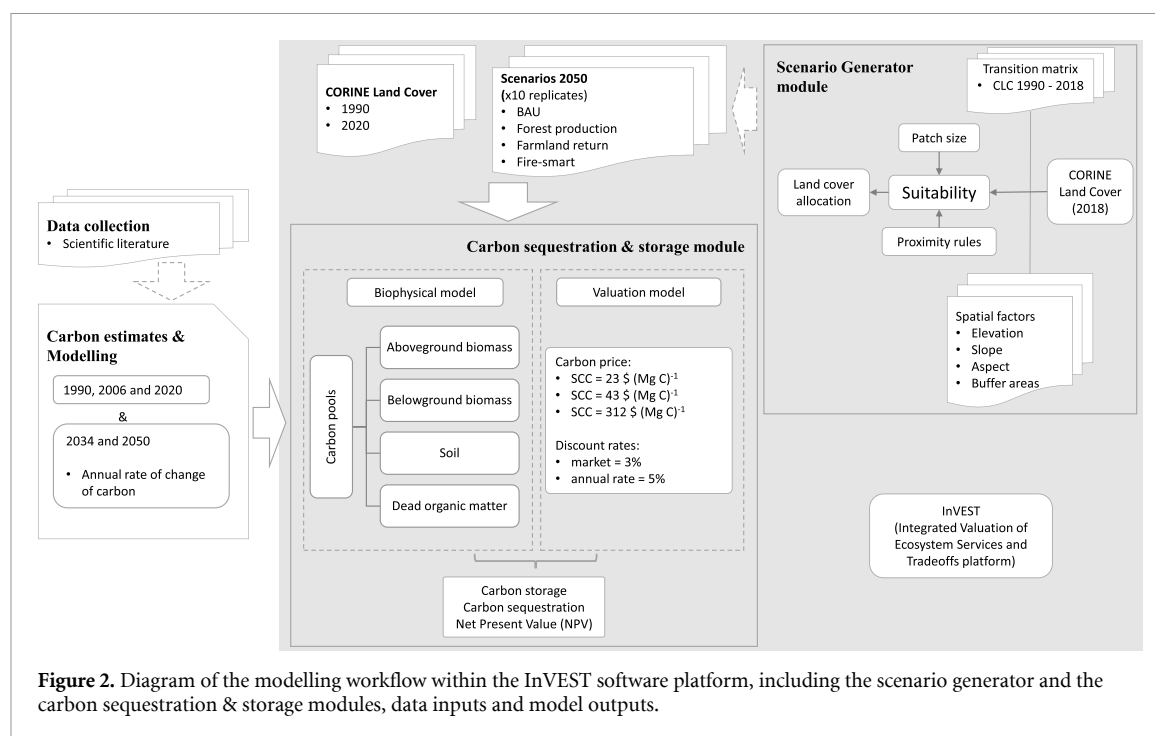


Figure 2. Diagram of the modelling workflow within the InVEST software platform, including the scenario generator and the carbon sequestration & storage modules, data inputs and model outputs.

Table 1. Description of the alternative landscape scenarios in the Transboundary Biosphere Reserve of Meseta Iberica for 2050.

Policy	Scenario	Description
Climate-smart	Rewilding (ReWild)	The future landscape modifications tend to follow past LULC change trends (1990–2018), allowing the simulation of potential EU climate-smart policies to boost natural regeneration through rewilding strategies. Socio-ecological processes, namely rural exodus and consequent land abandonment, are the main drivers of landscape change in this scenario. Therefore, an increase in semi-natural areas is expected (e.g. grasslands and shrublands), while agro-pastoral areas are projected to decline.
	Afforestation (Afforest)	Afforestation activities, as well as the restoration of riparian areas or the process of ecological succession, are responsible for the main changes in the landscape. In this scenario, afforestation actions favour forest species (e.g. coniferous species, such as <i>Pinus pinaster</i> , and deciduous/broad-leaved species, such as <i>Quercus pyrenaica</i>), emulating recent EU climate-smart policies to stimulate tree planting, restoration and development of renewable energy sectors (e.g. wood production and bioenergy).
Fire-smart	Farmland recovery (FarmRe)	The effects of a potential return to traditional farming activities, e.g. supported by the EU Common Agricultural Policy, are simulated in this scenario. The main effects derive from the reinforcement of rural policies through economic incentives to revert farmland abandonment and promote sustainable agricultural management to support local development, fire mitigation and biodiversity conservation. Therefore, agro-pastoral areas are expected to increase, mainly in formerly semi-natural areas.
	Agroforestry recovery (AgroforestRe)	The mitigation of negative impacts of wildfires through integration of agroforestry activities with current and/or former agricultural activities is simulated in this scenario. This scenario is based on the disruption and replacement of highly flammable cover types in order to decrease landscape flammability while maintaining the sustainable development of the region. Therefore, this scenario is based on a mixed system of agro-pastoral and agroforestry systems, simulating increases of the most relevant agroforestry cultures in the study area (e.g. sweet chestnut groves), as well as a moderate increases of farmlands. Also, semi-natural and forest areas (particularly coniferous forests) are forced to decrease, in order to simulate potential fire-smart policies in the future.

for Ecosystem Services; Sherrouse *et al* 2011), the InVEST is a relatively simple and low data demanding open-source modelling platform that provides consistent models (e.g. carbon storage and sequestration model) and support tools (e.g. scenario generator), being frequently applied to assess a varied spectrum of ecosystem services at different geographical scales (e.g. Grêt-Regamey *et al* 2017, Chaplin-Kramer *et al* 2019, Hamel *et al* 2021). Future land cover transitions (2020–2050) were modelled using information on past land cover transitions (1990–2018), as well as proximity-based constraints and several spatial layers to improve the allocation of new land cover areas within the study area.

2.3. Carbon modelling framework

The effect of LULC changes on CRES was assessed both in biophysical and economic dimensions by applying a scenario and modelling approach using the *Carbon Storage and Sequestration* module of InVEST (Sharp *et al* 2018; figure 2). The amount of carbon stored and sequestered was assumed as a proxy of the supply of CRES (Haines-Young and Potschin-Young 2018), whereas the avoidance cost damage approach was used by taking the social cost of carbon (i.e. the economic cost of an additional ton of carbon emitted to the atmosphere; Nordhaus 2011) as a proxy for the avoided economic damage due to a reduction in carbon emissions (Nelson *et al* 2009, Pascual *et al* 2010).

The biophysical and economic assessment of the CRES was carried out in two periods: between 1990 and 2020, and between 2020 and 2050. The calibration of the InVEST Carbon module was based on published data available for a watershed within the reserve (Sil *et al* 2017). The data were used to estimate carbon stocks in seven major land cover classes, namely agriculture, agroforestry, forest (deciduous, coniferous and mixed) and semi-natural (grasslands and shrublands). Four carbon pools were considered, the above- and belowground biomass, litter, and soil organic carbon. Since the available data included several subclasses of the main land cover classes defined for this study, the average of the carbon stocks of the subclasses was assigned to the corresponding major class in order to be used in the simulations.

Besides the effect of the spatial distribution of land cover changes over time, biomass growth and accumulation of organic carbon in the soil were also considered in the simulations by varying the carbon stocks in forest and semi-natural classes. The variations in accumulated carbon in each LULC class over time is automatically calculated by the model InVEST. The modelling platform calculates the net change in carbon storage over time in each pixel by applying the model to the current landscape and the landscape scenarios projected for the future. However, the other land cover classes were kept constant in the simulations. For instance, urban areas were kept constant since there is no data available concerning

additional urbanization for the study area. Also, the fraction of the reserve covered by urban structures is not substantial, and it is expected to continue so during the next decades due to the current socio-economic problems and land abandonment tendencies that affect most of the reserve.

The simulations of LULC change between 1990 and 2020 were conducted using data of carbon stock values for the same temporal period (1990–2020), applied to each LULC class. Carbon stocks for future LULC changes (2020–2050) simulations were computed according to estimates for 2020 plus the annual rate of carbon change calculated between 2006 and 2020 (adjusted for a total period of 30 years). Future carbon stocks and annual rate of change were calculated using equations (1)–(3):

$$CRate = \frac{(Cstock2020 - Cstock2006)}{(2020 - 2006)} \quad (1)$$

$$Cstock2035 = Cstock2020 + (CRate \times (2035 - 2020)) \quad (2)$$

$$Cstock2050 = Cstock2035 + (CRate \times (2050 - 2035)) \quad (3)$$

where Cstocks represent carbon density ($Mg\ C\ ha^{-1}$) for a given year, and CRate is the annual rate of change of carbon ($Mg\ C\ ha^{-1}\ yr^{-1}$), in this case, between 2006 and 2020.

Additionally, land cover transitions were assumed to take place in the mid-period analyzed, i.e. in 2006 (for 1990–2020) and in 2034 (for 2020–2050). Since InVEST considers only two periods, an intermediate date was used to estimate carbon stocks over time, in order to smooth change on carbon levels due to land cover transitions. As a result, the carbon stocks of transitions involving the agroforestry, forest and semi-natural land cover classes were assigned based on the available estimates for the carbon stocks in the year 2006 (for the period between 1990 and 2020) and the estimates computed for the year 2034 using equations (1) and (2) (for the period between 2020 and 2050). In the end, a total of 46 land cover classes were used in the simulations.

In order to cover the uncertainties associated with the estimations of carbon value, the valuation of the avoided economic damages was carried out by applying three Social Costs of Carbon (SCC) with a wide range of prices, all of them based on estimates available in published scientific literature, namely $SCC = 23\ \$\ Mg\ C^{-1}$ (Nordhaus 2011); $SCC = 44\ \$\ Mg\ C^{-1}$ (Tol 2008); and $SCC = 312\ \$\ Mg\ C^{-1}$ (Stern and Stern 2007). The application of SCC is a valuable approach in the policy-making context, since it allows to estimate the extra costs associated with carbon emissions that are not automatically reflected in market prices to better

compare the costs and benefits of specific environmental policies. In this approach, we considered the SCC as a proxy of the economic damage avoided, or the monetary benefits that the society can obtain from the carbon emission reduction, which can be related to the additional metric of ton of carbon sequestered from the atmosphere. Two discount rates were considered (i.e. the rate in which the monetary value of carbon sequestration will vary or decline over time, in order to simulate the society preference for payments that occur sooner rather than later), a market discount rate of 3% (Valatin 2011) and an annual rate of change in the price of carbon of 5% (Nelson *et al* 2009), which were kept constant in the simulations. A total of 123 simulations were run using the carbon sequestration and storage module of InVEST (1 past dates \times 3 SCC prices + 4 future scenarios \times 10 replicates \times 3 SCC prices).

Finally, the differences in the total carbon storage and sequestration among scenarios were statistically analyzed by applying the Kruskal–Wallis H test, followed by a mean rank multiple comparisons for $\alpha = 0.05$, using Dunn's pairwise tests with Bonferroni error correction.

2.4. Species distribution models

A complete series of species distribution models for 207 species (168 birds, 24 reptiles and 15 amphibians) using climate-only variables were obtained from previous published data (see Campos *et al* 2021b; see appendix C). The data include species distribution models for the Iberian Peninsula from four climate datasets (hereafter 'climate models'), and consequently projected for the reserve in 2050 under two future representative concentration pathways (RCP 4.5 and RCP 8.5; Campos *et al* 2021b).

In order to measure the impacts of each land management scenario on local biodiversity, a new series of species distribution models were built herein using the 'biomod2' R package (see Thuiller *et al* 2009). These models (hereafter 'habitat models') were developed for all species (appendix C), using LULC and topographic variables for the approximate period of the biodiversity data used in the climate models (i.e. year 2006). LULC data were obtained from the CLC database at 100 m resolution and reclassified to ten land cover classes (see appendix A). Topographic variables (altitude, slope and aspect) were derived from digital elevation data from the Shuttle Radar Topography Mission (SRTM) at 30 m spatial resolution (www.usgs.gov). LULC information (percentage of each class) was obtained from (a) the CLC maps for past conditions (2006) and (b) landscape simulations for 2050, for each land management scenario. The individual-species habitat models were built for the Iberian Peninsula at 10 km resolution, according to the methodological steps applied in Campos *et al* (2021b). The predictive accuracy of the species distribution models was

evaluated through the area under the curve (AUC) and the true skill statistic (TSS), two frequently used and consensual evaluation metrics available in 'biomod2' R package (see Thuiller *et al* 2009). The models were then projected to the reserve at 1 km resolution for a past (2006) and future (2050) periods, under the four landscape scenarios (ten replications per scenario). Finally, ensemble model predictions were reclassified into binary presence/absence maps through ROC (receiver operating characteristic) optimized thresholds available in 'biomod2' (see Thuiller *et al* 2009). The impacts of climate and land management scenarios on biodiversity were measured through the number of species predicted to register loss, gain or no change in suitability between 2005 and 2050 (at pixel level). All analyses were performed considering climate models (using average predictions of four models; see Campos *et al* 2021b), habitat models, and the combination of climate and habitat models (i.e. spatial agreement of species presence/absence predicted by both models).

3. Results

3.1. Land-use/cover change

The analysis of the LULC changes revealed a decline in forest and agroforestry areas and an increase in semi-natural areas (grasslands and shrublands), water and urban areas between 1990 and 2018 in the study area (figure 3). Projections predict an increase of grasslands (23%) and shrublands (19%), and a decrease in agroforestry and deciduous (of almost 40% each), conifers (32%) and agro-pastoral (around 20%) systems for 2050 under the rewilding scenario (figure 3 and appendix D).

In contrast, policies promoting afforestation are predicted to increase deciduous (40%) and coniferous (70%) forests, while shrubland areas are expected to decrease by almost 36% (figure 3 and appendix D). The management strategy focused on promoting agricultural activities was predicted to increase agro-pastoral areas by almost 15% (see 'FarmRe' scenario in figure 3 and appendix D). Grasslands were predicted to have the highest decrease (almost 50%) in this scenario, while shrublands are expected to experience a decrease of approximately 13%. Finally, the 'AgroforestRe' scenario is predicted to lead to an increase in more than 50% of agroforestry areas, while reducing around 10% of both grasslands and shrublands (see 'AgroforestRe' scenario in figure 3 and appendix D).

3.2. Carbon storage

Land cover changes in the reserve between 1990 and 2020 contributed to an increase in total carbon stored in the landscape (figure 4(A) and appendix E). In this period, the mean carbon density increased from 43.79 to 68.7 Mg C ha⁻¹, a growth of

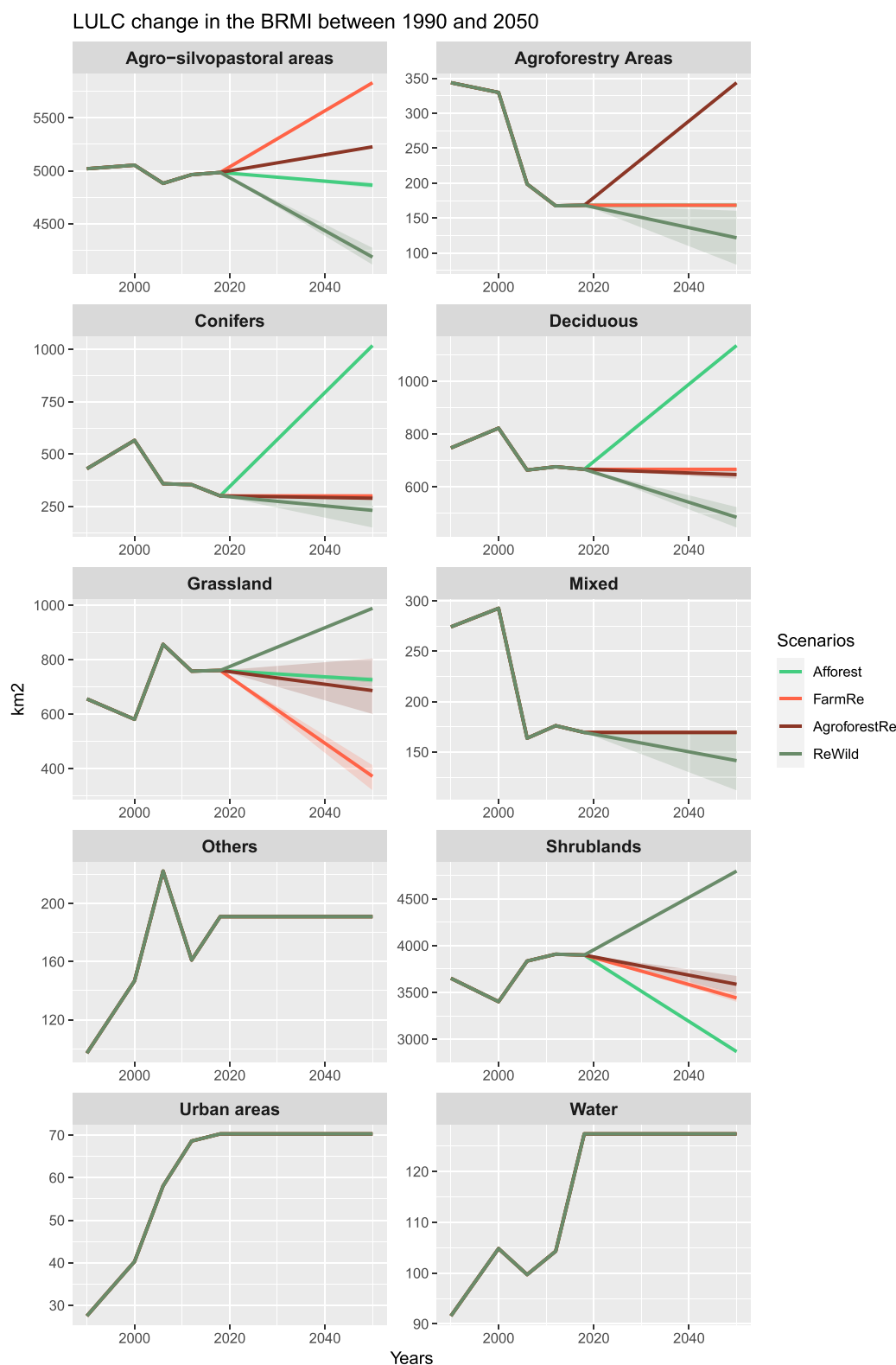
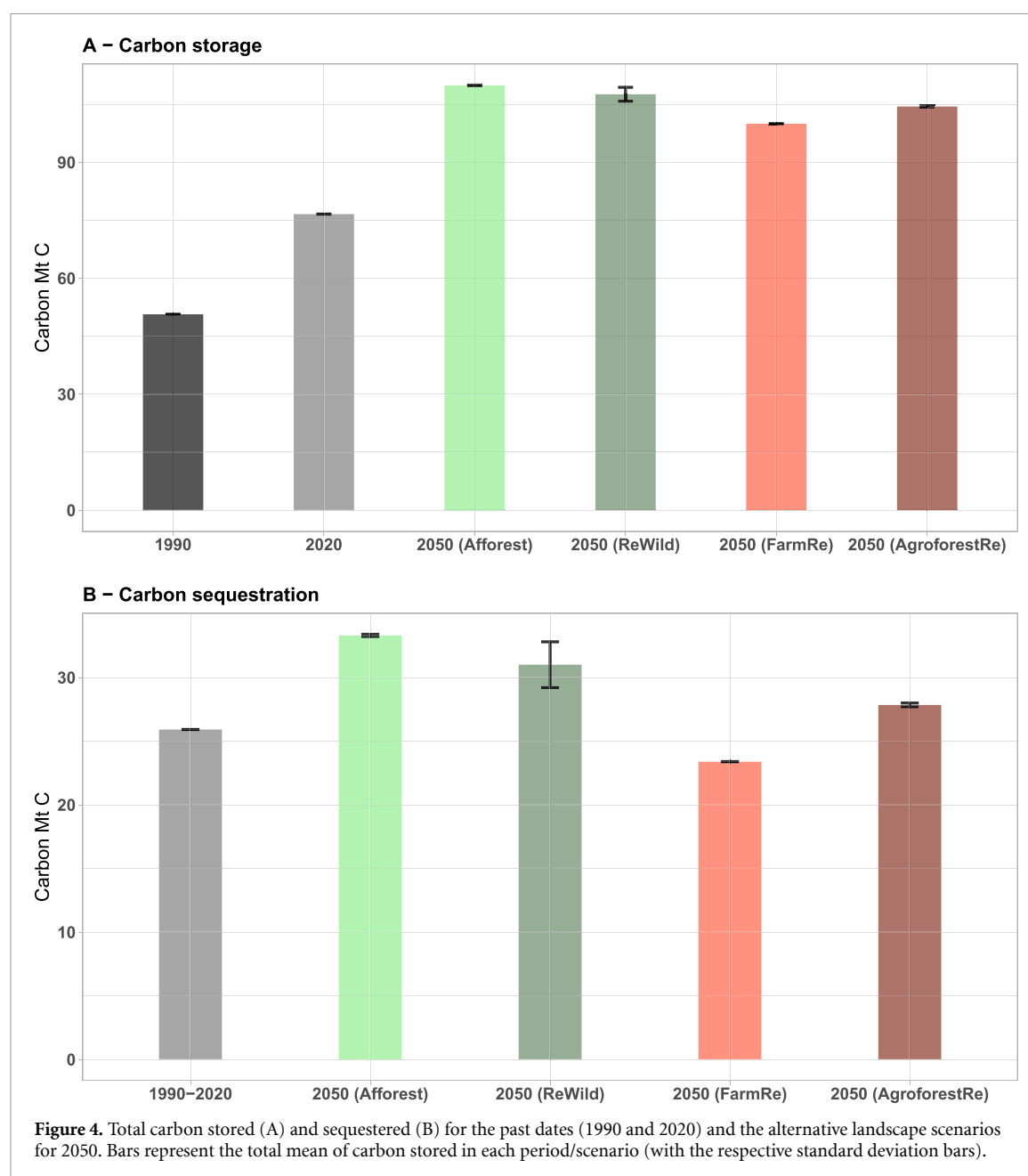


Figure 3. Observed and projected land cover change (km²) from 1990 to 2050 in the Biosphere Reserve Meseta Ibérica.

approximately 57%. The projected landscape changes are expected to increase the total carbon stored for the 2050 scenarios (figure 4(A) and appendix E), although we found differences among scenarios ($p < 0.001$). The climate-smart scenarios ('Afforestation' and 'ReWild') presented the highest amount of carbon stored in the landscape, and the

'FarmRe' scenario the lowest among all scenarios (figure 4(A) and appendix E). Differences in the total carbon stored between both climate-smart scenarios and the 'FarmRe' scenario were significantly different ($p < 0.001$). The 'AgroforestRe' scenario showed higher values than the 'FarmRe' scenario, but still lower than the climate-smart scenarios. Only



the differences between ‘AgroforestRe’ and ‘Afforest’ scenarios were significantly different ($p = 0.002$). The mean carbon density (figure 4(A) and appendix E) also increased in all future scenarios, although with lower variation (ranging from 28% to 41%) compared to the past period.

3.3. Carbon sequestration

The total amount of carbon sequestered in the reserve increased with the past changes in LULC between 1990 and 2020. Carbon sequestration increased in general in the future alternative scenarios (2020–2050), except for the ‘FarmRe’ scenario, in which the estimated amount is smaller than in the previous 30 years (figure 4(B) and appendix F). The effect of LULC changes on total carbon sequestered differed among scenarios (figure 4(B) and appendix F), particularly between ‘FarmRe’

and climate-smart scenarios ($p = 0.000$ in both ‘Afforest’ and ‘ReWild’ scenarios), and between ‘AgroforestRe’ and ‘Afforest’ ($p = 0.002$). Mean carbon sequestration rate increased between the past period ($0.83 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) and the future scenarios (figure 4(B) and appendix F), particularly for the climate-smart scenarios (0.98 ± 0.00 and $0.91 \pm 0.05 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, for the ‘Afforest’ and ‘ReWild’ scenarios, respectively), while ‘AgroforestRe’ presented a similar value ($0.82 \pm 0.00 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) and ‘FarmRe’ a lower sequestration rate ($0.69 \pm 0.00 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Considering the full time period of analysis (1990–2050), the ‘Afforest’ scenario sequestered the largest amount of carbon (56.91 Mt C), followed by ‘ReWild’ and ‘AgroforestRe’ (56.91 and 53.75 Mt C, respectively), while ‘FarmRe’ sequestered the least (49.29 Mt C).

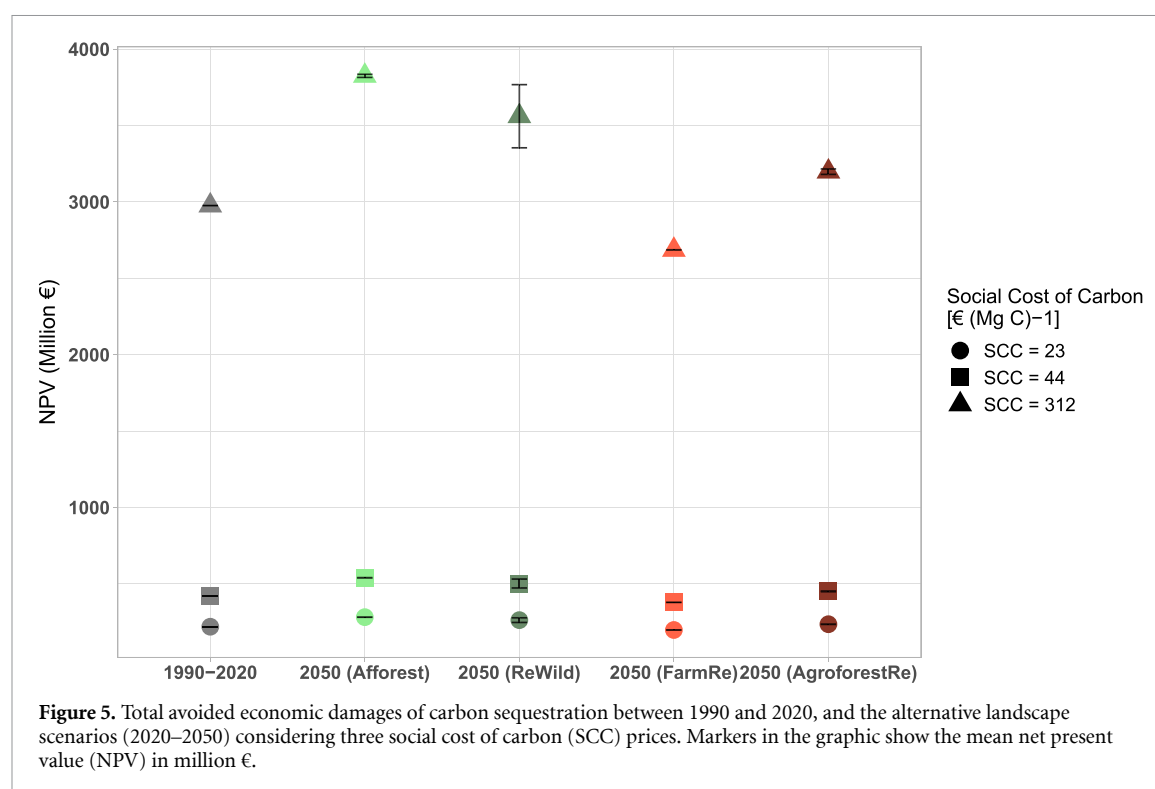


Table 2. Predictive accuracy metrics of the species distribution models (climate and habitat models). The AUC and the TSS metrics are summarized (mean and standard deviation), according to taxonomic groups.

	Climate models ^a		Habitat models	
	AUC _{mean}	TSS _{mean}	AUC _{mean}	TSS _{mean}
Birds	0.952 ± 0.03	0.791 ± 0.11	0.946 ± 0.04	0.778 ± 0.12
Amphibians	0.952 ± 0.02	0.771 ± 0.07	0.950 ± 0.03	0.783 ± 0.10
Reptiles	0.951 ± 0.03	0.805 ± 0.11	0.929 ± 0.05	0.733 ± 0.14

^a Models obtained from Campos *et al* (2021b).

3.4. Valuation of avoided economic damages

The avoided economic damages derived from carbon sequestered in the reserve ranged from 198.0 M€ [SCC = 23 € (Mg C)^{−1}] to 3825.2 M€ [SCC = 312 € (Mg C)^{−1}]. Additionally, the economic benefits of carbon sequestration tend to increase between the past (1990–2020) and future (2020–2050) periods, except for the ‘FarmRe’ scenario (figure 5). Considering the full time period (1990–2050), the highest monetary values correspond to the climate-smart scenarios (ranging from 501.4 to 6801.5 M€ in the ‘Afforest’ scenario and 481.9–6537.4 M€ in the ‘ReWild’ scenario). The ‘AgroforestRe’ scenario had an intermediate value (256–3476.3 M€), while ‘FarmRe’ had the lowest value (215–2919.5 M€).

3.5. Species distribution under climate and land management scenarios

Climate and habitat models had high and similar predictive performances (climate models—AUC_{mean} = 0.952, SD = 0.03; TSS_{mean} = 0.791, SD = 0.11; habitat models—AUC_{mean} = 0.944, SD = 0.04; TSS_{mean} = 0.774, SD = 0.12; see table 2 and appendix C for details). Additionally, the

predictive accuracy of models was high for all taxonomic groups (table 2).

Model projections revealed a wide range of species responses, a pattern observed for both climate, habitat and combined models (appendix G). Overall, more species were predicted to lose climate suitability than habitat suitability (appendix G). The number of species negatively affected by climate change increased from approximately 53% to 62% under the RCP 4.5 and RCP 8.5 scenarios, respectively. The habitat models indicated that a considerable number of species are unaffected by land management strategies, and most of the species were predicted to lose suitability when both climate and habitat models are combined (appendix G).

However, when analyzed in terms of percentage of suitability changes, most species benefit mainly from climate-smart scenarios (figure 6). These results are consistent amongst taxonomic groups and between species in different conservation status categories. The ‘Afforest’ scenario retrieved the highest suitability gains for vulnerable (VU) amphibians and vulnerable and near-threatened (NT) birds, independently of the climate change scenario

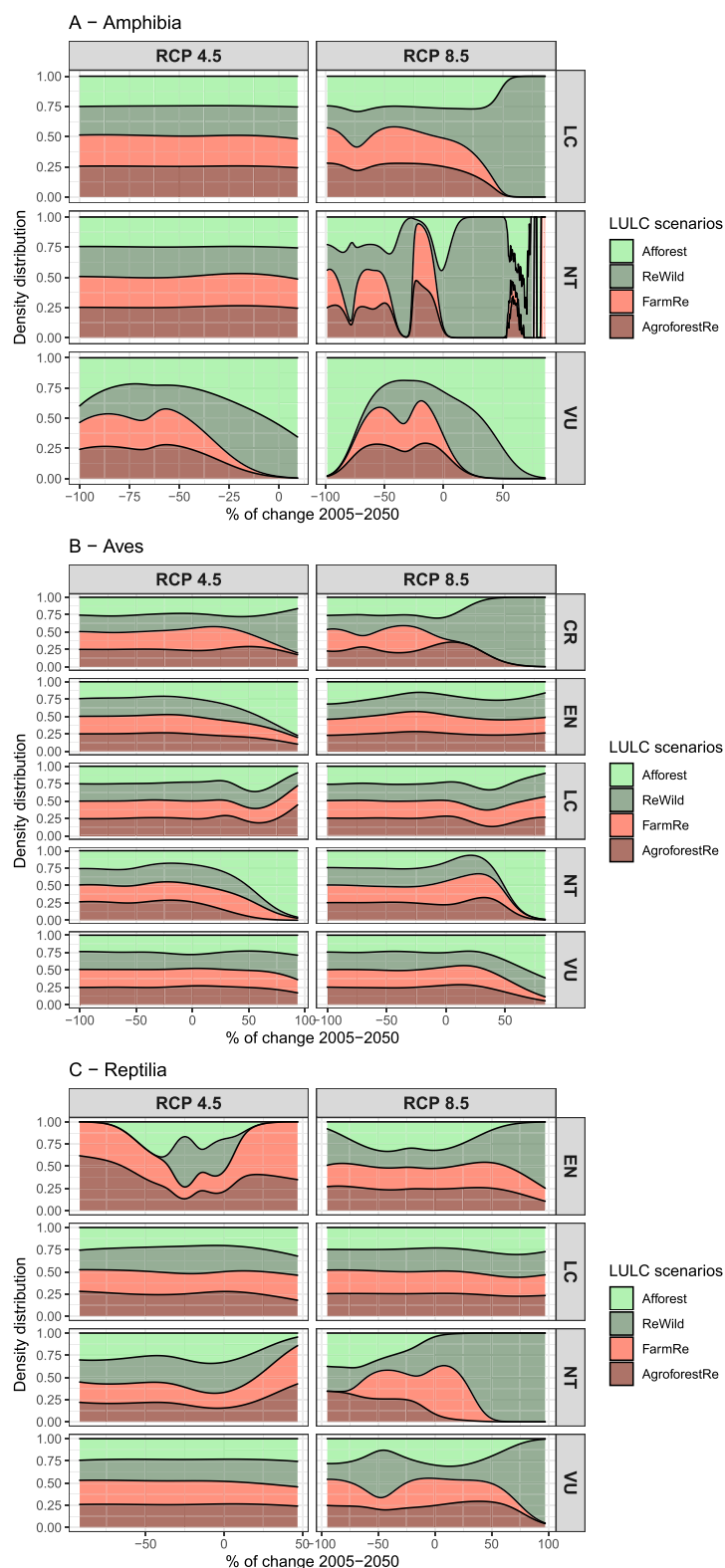


Figure 6. Density distribution plots, representing the variation of a histogram using the kernel density estimation of the variable probability density function to smooth the noise associated with the distribution of habitat availability tendencies of the species groups. Results are presented for the combined climate-habitat suitability change between 2005 and 2050 (%). The density plot peaks indicate the intervals where the climate-habitat suitability change is more concentrated, relative to all land management scenarios. Data grouped by taxonomic group ([A] amphibians, [B] birds, and [C] reptiles), regional IUCN status for Portugal and Spain (the most concerning status was considered in cases where regional classification differed between countries; CR—critically endangered; EN—endangered; VU—vulnerable; NT—near-threatened; LC—least concern), and (RCP 4.5 and RCP 8.5).

(figures 6(A) and (B)). The ‘ReWild’ scenario stood as the most relevant for most reptiles, mainly for species with the most concerning conservation

status (near-threatened, vulnerable and critically endangered [CR] taxa; figure 6(C)) and critically endangered birds (appendix H). These effects tend

to increase in the worst-case climate change scenario, by providing the highest suitability gains in comparison to the remaining scenarios. The fire-smart scenarios appeared to be particularly important for species distribution suitability under the RCP 4.5 scenario, providing the highest percentage of gains for several bird species of least-concern (LC) and endangered reptiles. However, the fire-smart scenarios became also relevant for species with open-habitat preferences, with both 'AgroforestRe' and 'FarmRe' providing the highest suitability gains under the two RCP scenarios for open-habitat birds of conservation concern (near-threatened and vulnerable species; appendix H).

4. Discussion

Overall, three main findings should be pinpointed in the light of the results presented here: (a) climate-smart scenarios provide higher rates of carbon sequestration and storage than fire-smart policies; (b) climate-smart scenarios prevent more economic damages due to carbon emissions reduction than fire-smart scenarios; (c) climate-smart scenarios provide more benefits for species of conservation concern (climate-habitat suitability), while fire-smart scenarios are beneficial for a large number of species adapted to semi-natural habitats under future climate change.

4.1. Climate regulation services under climate- and fire-smart policies

The results indicate that the implementation of climate-smart policies, both focused on large-scale afforestation strategies and rewilding initiatives, are predicted to better sustain climate regulation services in the forthcoming decades in comparison to fire-smart policies (figure 4). The improvement of the CRES under these scenarios is also more economically advantageous in comparison to both fire-smart approaches tested herein (figure 5). These results suggest that EU policies that could take advantage of current rural abandonment or that focus on the landscape ecological restoration could be more advantageous (in terms of climate regulation services and economic damages avoided by the additional carbon emitted to the atmosphere) than alternative policies fomenting the return of agriculture or agroforestry activities in the region (see Briner *et al* 2013, Sil *et al* 2017). Despite these results, two considerations should be emphasized and explored in future studies. Firstly, the potential impacts of climate-smart scenarios on wildfires and the consequent negative impacts on carbon storage and sequestration. The putative increment of large and severe fires under climate-smart scenarios might boost the emission of carbon stored in forested and rewilded areas, while carbon sequestration might become significantly compromised during periods of post-fire

recovery. Secondly, intensified fires derived from climate-smart scenarios might increase economic costs (e.g. damage costs and higher investments in fire suppression). These potential climate-smart disadvantages might even exceed the carbon and economic benefits observed herein, and further support fire-smart strategies in the future. Also, according to the obtained land-use tendencies, a higher food production is expected under the FarmRe (agricultural products) and AgroforestRe (e.g. chestnuts) scenarios. As such, the analyses of food production and other provisioning services that might be boosted by fire-smart scenarios, should also be contemplated and evaluated from an economical point of view in future studies.

Still, future planning should consider the landscape dynamics and heterogeneity of the region demanding urgent and contextualized interventions (Sheffer 2012). In this context, it is advisable to consider other relevant ecosystem services and functions, such as fire regulation and protection capacities, in which fire-smart management could be preferable by generating more opportunities for fire suppression (especially under a 'FarmRe' strategy) and fire-resilient landscapes, while securing the sustainable supply of the CRES, particularly under a 'AgroforestRe' strategy, through conversion of pine forest to broad-leaved forest and increase of other agroforestry systems (Pais *et al* 2020).

4.2. Biodiversity conservation under climate- and fire-smart policies

The biodiversity models indicated a high variability of species responses, with contrasted dissimilarities between climate-smart and fire-smart policies. This variability might be explained by the complex interactions between climate and land-use change that may lead to synergistic, additive, or antagonistic effects on biodiversity communities with distinct climatic and habitat preferences (Newbold 2018, Northrup *et al* 2019). In this context, this study underlines the need for combining the effects of climate and LULC change, whose spatial interactions are often neglected or oversimplified in modelling approaches, to produce more robust predictions of species status and trends (Sirami *et al* 2017), and ultimately contribute to landscape planning capable of effectively assisting biodiversity conservation.

Overall, climate-smart policies were predicted to be particularly advantageous for several taxa of conservation concern in the study area (figure 6 and appendix H). Taking advantage of current rural abandonment trends in these areas to implement or reinforce existing rewilding initiatives (e.g. the Greater Côa Valley rewilding initiative in the Transboundary Biosphere Reserve of Meseta Iberica; <https://rewildingeurope.com/>), could be a nature-based solution to promote more sustainable landscapes able to protect threatened species

(Campos *et al* 2021a). However, climate-smart strategies (and rewilded landscapes in particular) are favourable to a majority of species preferably adapted to humid woodlands and forested areas in detriment of several open-habitat species, a pattern already observed in other biosphere reserves of the Iberian Peninsula (e.g. Pais *et al* 2020, Campos *et al* 2021a). Nonetheless, the impacts of climate-smart scenarios on large wildfires and the consequent damaging effects on biodiversity and habitat availability (e.g. predicted available habitats might become unsuitable after burning) should be assessed in future studies.

In contrast, fire-smart policies were predicted to benefit another spectrum of biodiversity, particularly bird species with open-habitat preferences (such as grasslands and wetlands; figure 6 and appendix H). Moreover, fire-smart policies tended to positively affect these species independently of climate change scenarios (figure 6 and appendix H). Some species are even benefited by intensified climate change effects, which could be probably related to the larger proportion of warm-dwelling bird species usually adapted to early successional habitats (Regos *et al* 2016). In fact, the extensive agricultural and semi-natural areas that dominate the landscapes of the reserve (currently occupying approximately 50% of the reserve; see figure 3) provide suitable habitat conditions for a large number of species. Adopting fire-smart strategies, either by reinforcing current EU agricultural policies or by stimulating more diversified landscapes through integration of agroforestry and agricultural activities, would allow protecting these species communities adapted to the dominating human-mediated habitats of the study area, while supporting fire mitigation and regulation at the same time (see Lomba *et al* 2020).

4.3. Recommendations for climate-smart and fire-smart policies

According to these results, climate-smart landscapes appear to be the land management strategy that benefits the most objectives (CRES and individual species) in the study area. The landscape natural regeneration derived from the intensified rural abandonment in the region, which also represents historical and contemporary landscape change tendencies shared by several rural mountains across Europe (Otero *et al* 2015), might facilitate the implementation of such strategies. However, the application of climate-smart strategies under the current EU policies on natural restoration (supported by large-scale afforestation actions) should be carefully planned (Hermoso *et al* 2021). Future planning should contemplate potential ecological impacts, particularly related to decreases in landscape heterogeneity (e.g. loss of agricultural and other semi-natural habitats) and escalation of fire hazard (see Aquilué *et al* 2020), both increasingly significant in Mediterranean regions

(Moreira *et al* 2020). Also, these strategies should be carefully evaluated to avoid causing more harm than good, and even risk the benefits for which they were implemented in the first place. As an example, the conversion of landscapes historically dominated by extensive farming to afforested climate-smart landscapes might counterproductively disrupt carbon sequestration and storage processes secured by existent semi-natural habitats. In effect, previous studies alert for the crucial role of perennial grasslands, peatlands and wetlands as effective carbon sinks that also contribute to reducing landscape emissions (Scherr *et al* 2012, Bond *et al* 2019), and in some cases more efficiently than forested areas (Dass *et al* 2018). Additionally, potential increase of fire hazard and severity induced by climate-smart approaches could exacerbate the environmental and socioeconomic impacts of extreme wildfires, and also contribute to deplete carbon sinks and intensify carbon emissions (Bond *et al* 2019). Although these potential trade-offs were not estimated herein, we recommend that future studies should further quantify the potential detrimental effects of climate-smart strategies on the CRES (and other services, such as fire regulation) and biodiversity.

In this context, implementing fire-smart strategies could also provide sustainable solutions targeting the supply of climate regulation services and biodiversity conservation, while maintaining a heterogeneous landscape and allowing gradual conversion of local areas to more fire-resilient and fire-resistant landscapes (Kelly *et al* 2020, Pais *et al* 2020). In fact, fire-smart strategies might stand as less risk prone in comparison to climate-smart policies, by preventing higher economic, social and environmental costs resulting from intensified wildfires. The integration of EU agricultural and rural policies could also be viewed as complementary management strategies, particularly in landscapes spatially and temporally shaped by agriculture (Lomba *et al* 2020). Maintaining agro-pastoral areas would allow protecting several biological communities and associated semi-natural habitats, which are also extremely viable not only for supporting climate regulation services (e.g. preservation of important carbon sink systems, such as perennial grasslands), but also for securing another spectrum of ecosystem services that might be disfavoured by climate-smart policies (e.g. provisioning, fire control/protection services). Having into account the predicted trade-offs between climate- and fire-smart strategies, future landscape planning should contemplate economic compensations to alleviate the potential negative impacts that each land management conveys if implemented. The economic benefits of the CRES under climate-smart strategies could allow increased investments in preventive fire management, while the socio-economic development associated with the implementation of fire-smart strategies could be attended by increased

investments in the conservation of rewilded habitats. Necessarily, the successful implementation of such management policies should consider the spatial-temporal interaction of dynamic landscape factors and their consequent impacts on ecosystem services and biodiversity.

4.4. Limitations and sources of uncertainty

The results presented herein should be analyzed with caution due to several limitations and sources of uncertainty. A major limitation of the modelling approach conducted to simulate the landscape scenarios and the carbon storage and sequestration is the oversight of climate change effects, since the models did not explicitly include climatic factors in the analyses. Several studies have predicted considerable shifts in vegetation dynamics and distribution across Europe due to climate change effects (e.g. Neumann *et al* 2017, Wu *et al* 2021). As such, assessing how climatic variability affects LULC change, and how it contributes to negative or positive feedbacks on CRES, should be quantified in future landscape modelling approaches. Also, future modelling approaches should consider the potential saturation effects of carbon sequestration (see Nabuurs *et al* 2013), which might inclusively reduce the benefits of climate-smart strategies in the CRES, and thus, balancing the overall differences between climate-smart and fire-smart scenarios. Another potential limitation of our models is related to the assessment of the CRES as the only ecosystem service scrutinized in this work. Having into account the extreme fire regimes of the study area that is estimated to escalate in the next decades due to climate change (Dupuy *et al* 2020), and how alternative land management scenarios might modify the impacts of fire at the landscape level, future studies should investigate how these nature-based solutions could enhance services such as fire regulation capacity, by including fire regimes and fire management solutions (e.g. evaluation of fire suppression strategies) in the modelling procedures. Future works should also focus on a wider range of ecosystem services that might be benefited by these alternative land management strategies, such as wood production, food availability, and water regulation.

Regarding the species distribution models, and because of general criticisms associated with the conversion of continuous model outputs into binary predictions, the model projections were also analyzed according to continuous prediction values based on the integration between both habitat and climate models. The integration was performed using the mean values of the ensemble models (habitat and climate models), weighted by the ROC of each ensemble model (results not presented in this work). However, since there were no significant differences in comparison to the results obtained with the binary predictions, the latter approach was used in the final analyses as it provides more intuitive and

interpretable results. Still, these results should be interpreted with confidence since the classification thresholds available in 'biomod2' are already optimized and are consensually used in several studies (e.g. Thuiller *et al* 2009, Hao *et al* 2019, 2020). Also, the selected thresholds were slightly conservative regarding the classification of predicted presences, which has been referenced as an advisable approximation in regional/local models built with precise data for characterizing accurate ranges in protected areas (Vale *et al* 2014). Other limitations of the species distribution models built in this work reside in the potential uncertainties associated to model downscaling, particularly related to the projections of the Iberian models (built at 10×10 km of spatial resolution) to the Biosphere Reserve (1×1 km). Nonetheless, this approach has been widely applied with consistent results for capturing general environmental patterns that allow predicting potential distributions at regional and local scales with accuracy (Araújo *et al* 2005).

5. Conclusions

This study contributes to a better understanding of the potential impacts of alternative land management policies on climate regulation services and biodiversity conservation in regions undergoing increased environmental change. Climate-smart scenarios were predicted to deliver the highest rates of carbon sequestration and storage, and also to prevent more economic damages due to carbon emissions reduction in comparison to fire-smart scenarios. Also, climate-smart scenarios were predicted to deliver more benefits for species of conservation concern. In contrast, fire-smart scenarios were predicted to secure the habitat suitability of species adapted to semi-natural habitats under future climate change. This study provides valuable data to support a more informed landscape planning and decision making in abandoned rural mountains in Southern Europe. Still, this study should be complemented with the analyses of other regionally relevant ecosystem services (e.g. fire regulation), which would contribute to a wide-ranging risk assessment needed for the successful implementation of these alternative nature-based solutions.

Data availability statement

The data that support the findings of this study are openly available at: <https://doi.org/10.5281/zenodo.4589376>; <https://doi.org/10.5281/zenodo.4599822>.

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