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Original Research Article

Alternative pathways to a sustainable future lead to contrasting biodiversity responses

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ABSTRACT

Land-use change is currently the main driver of biodiversity loss. Projections of land-use change are often used to estimate potential impacts on biodiversity of future pathways of human development. However, such analyses frequently neglect that species can persist in human-modified habitats. Our aim was to estimate changes in biodiversity, considering affinities for multiple habitats, for three different land-use scenarios. Two scenarios focused on more sustainable trajectories of land-use change, based on either technological improvements (Pathway A) or societal changes (Pathway B), and the third reflected the historical or business-as-usual trends (Pathway 0). Using Portugal as a case study, we produced spatially-explicit projections of land-use change based on these pathways, and then we assessed the resulting changes in bird species richness and composition projected to occur by 2050 in each of the scenarios. By 2050, alpha and gamma diversity were projected to decrease, relative to 2010, in Pathway 0 and increase in Pathways A and B. However, different pathways favored different species groups, and presented strong regional differences. In the technological improvement pathway, loss of extensive agricultural areas led to an increase in both natural and extensive forest areas. In this pathway, forest species increase at the expense of farmland species, while in the societal change pathway the reverse occurs, as extensive agricultural areas were projected to increase. We show that while multiple positive pathways (A and B) for biodiversity can be envisioned, they will lead to differential impacts on biodiversity depending on the transformational changes in place and the regional socio-economic context. Our results suggest that considering compositional aspects of biodiversity can be critical in choosing the appropriate regional land-use policies.

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1. Introduction

Species diversity has been declining steadily over the last century (Díaz et al., 2019). While biodiversity change has multiple drivers, habitat destruction via land-use change is considered to be the primary driver of changes in species richness and composition within terrestrial ecosystems (Pereira et al., 2012). In the future, the pressure on land is likely to increase, as global human population is expected to grow from around 7 billion in 2010 to 9 billion by 2050, thus increasing food consumption by 1.7 times and wood consumption by 1.3 times (van Vuuren et al., 2012). Such increase in consumption is likely to lead to further habitat conversion and associated biodiversity change. However, there is uncertainty as to how the increasing demand for goods will affect land-use dynamics in the future, and consequently biodiversity.

In order to reach global and national goals, such as the UN Sustainable Development Goals for 2030 (UN, 2015) and the goals and targets of the post-2020 global biodiversity framework of the Convention on Biological Diversity (CBD, 2020), policy- and decision-makers need tools to evaluate the effects of possible management actions and policy measures under future environmental conditions (Pereira et al., 2010; Rosa et al., 2017; Kok et al., 2017). Scenario analysis of alternative plausible futures (i.e., pathways of events under a set of key assumptions) is often used as a tool to explore and evaluate the extensive uncertainties associated with future land-use change and facilitate decision-making processes in conservation planning (Ferrier et al., 2016; Nicholson et al., 2019). Exploratory scenarios tend to examine the consequences of a persistence of 'business as usual' trends (i.e., population growth, economic growth, land-use change trends), as opposed to alternative "radical" actions (i.e., change in consumption patterns or land-use practices).

The key features of the scenarios' narratives are then translated by modelers into quantitative metrics of environmental drivers, such as land-use change (Popp et al., 2017). Biodiversity modelling approaches then translate such projections into expected consequences for nature, by exploring the impact of habitat loss and the conversion between broad land-use classes (van Vuuren et al., 2012; Titeux et al., 2016). Yet, these approaches often overlook fundamental processes. For instance, traditional species-area relationship (SAR) modeling approaches simplistically assume that all species are ecologically equivalent and constrained to their native habitat, and thus natural habitat modified by human activities cannot harbour native biodiversity (Pereira and Daily, 2006; Thuiller et al., 2013; Mendenhall et al., 2014). While some species are highly sensitive to habitat loss and only occur in native habitats, there is vast empirical evidence of extensive biodiversity persisting, and in some cases thriving, within the human-modified habitats (Newbold et al., 2015; Martins and Pereira, 2017; Frishkoff et al., 2019). In fact, the International Union for Conservation of Nature (IUCN) reports that at least 47% of extant bird species use human-modified landscapes, with 32% using agricultural habitats specifically (IUCN, 2017).

On the other hand, community composition often differs between undisturbed native areas and human-modified habitats (Pfeifer et al., 2017; Karp et al., 2018). For instance, compared with natural habitats, assemblages in disturbed habitats are shown to have more widespread species on average (Newbold et al., 2018), while farmland birds, seem to be particularly sensitive to agricultural intensification (Inger et al., 2015; Schipper et al., 2016). A common finding is that species responses to land-use change can vary considerably between and within species functional groups depending on whether the change in habitat actually affects the ability of the species to persist in the new landscape. For conservation planning, it is critical to include these differential responses of species to future changes in their habitat to ensure that scenarios can be used to support policy- and decision-makers targeting environmental protection and sustainable socio-economic development (e.g., vertebrates (Martinuzzi et al., 2015), carnivores (Kaim et al., 2019) and birds (Princé et al., 2015; Cannon et al., 2019). In agricultural regions across France, for example, agricultural intensification is expected to negatively impact generalist species that live in farmland, but have very little impacts on all specialist species other than grassland species. In contrast, a scenario based on extensification of agricultural systems (i.e., low-intensity agriculture) showed the greatest potential to reduce current declines in breeding birds (Princé et al., 2015). Moreover, it is important to understand the spatial patterns of habitat change and associated biodiversity change across the landscape.

Here we developed a framework based on the countryside SAR model (Pereira and Daily, 2006) to project the consequences of future land-use changes on species diversity under positive, but distinct, land-use trajectories and sustainable management strategies, using Portugal as a case study. The countryside SAR model, unlike other SAR approaches, accounts for the species' ability to persist in human-modified habitats when assessing and predicting biodiversity change across scales (but see Koh and Ghazoul, 2010), and has proven to outperform traditional SAR approaches when describing the number of species in human-modified landscapes (Proença and Pereira, 2013; Martins et al., 2014). Specifically, our objectives were to (1) quantify future changes in breeding bird species richness, including changes in richness of three functional species groups (i.e., forest species, farmland species and species with affinity for other natural habitats), under distinct positive land-use change scenarios; (2) compare national (gamma diversity) and grid cell level (alpha diversity) species responses, between and within these species' groups, under each scenario (3) evaluate which species groups will experience the most changes across regions under different scenarios; and (4) identify the regions where changing the management strategy could have the largest effects on different species groups. As part of this study, we also identified the species groups most vulnerable to future land-use change, if no change in policies is implemented (commonly referred to as a 'business-as-usual' scenario).

2. Methods

2.1. The pathways scenarios

Our analysis was based on two distinct sustainable transition scenarios developed by the EU FP7 project PATHWAYS (www.pathways-project.eu). The project aimed at exploring the possibilities for transitions into a low-carbon, sustainable Europe. These scenarios were designed to achieve a broad set of sustainable development objectives, (i.e., covering different aspects of environmental integrity, economic resilience, social well-being and good governance) based on existing international agreements (Table 1; van Sluisveld et al., 2016).

The first scenario, hereafter "Pathway A", is a technical component substitution scenario and assumes that targets for sustainability are achieved via large-scale technological improvements, without a full reordering of existing societal structures. In Pathway A, better yields and the development of precision farming (i.e., high efficient agriculture) allow for the intensification of agriculture in productive areas that are already being cultivated. As a result, there is an increase in the abandonment of less productive and marginal farmlands. Management practices that maintain early successional habitats increase natural areas, while more areas transition to extensive forest. This pathway would lead to a "land-sparing" approach with food and timber production focused on intensive agricultural and forestry areas, and with increased area for nature conservation and rewilding on abandoned farmland (Phalan et al., 2011; Merckx and Pereira, 2015).

The second scenario, hereafter "Pathway B", is oriented towards a stronger societal transformation. This scenario entails a shift to a new socio-technical system driven by societal changes impacting/influencing behavior and consumption patterns (e.g., lower meat and dairy consumption, reduction of waste). Moreover, in this scenario agriculture and nature protection are combined creating multifunctional landscapes. Such changes would lead to an extensification of the agricultural landscape. The co-occurrence of environmentally-friendly agricultural practices and nature conservation in this scenario promotes a "land-sharing" approach (Phalan et al., 2011).

Both Pathways were contrasted with a business-as-usual scenario, hereafter "Pathway 0", in which no new policies are introduced in order to specifically achieve sustainable development targets, i.e. the historical trends of land-use change were maintained into the future. For a full description of the assumptions of each Pathway see van Sluisveld et al. (2016).

2.2. The case study: Portugal

We investigated how biodiversity, in particular, resident breeding bird species richness (hereafter bird species richness), would respond to projected land-use change in Portugal up to 2050 in each scenario (i.e., Pathways 0, A and B). Portugal is an interesting case to study due to its socio-economic and ecological spatial heterogeneity and dynamic history of land-use change. Agriculture covers more than a third of the Portuguese national territory (MAMAOT, 2013a, 2013b), with cultivated lands dominated by cereal production and permanent crops. Since the 1960s, and due to a marked rural exodus, many agricultural lands (particularly small-scale farms) in the north of Portugal have been abandoned, leading to an increase in shrubland (e.g., *Erica sp*., *Ulex sp*., *Cytisus sp*) and native oak forest (*Quercus robur* and *Quercus pyrenaica*) patches due to natural succession. At the same time, agriculture practices in Portugal have intensified in more productive areas. In the south, less productive agriculture areas have been converted into extensive pastures. In contrast, the area occupied by the traditional *Montado* agro-forestry system, an evergreen oak woodland, where the predominant tree species are the cork-oak (*Quercus suber*) and holm-oak (*Quercus ilex*), remained relatively unchanged, due to its strong economic and cultural value (Pereira et al., 2009; Jones et al., 2011; INE, 2011; Levers et al., 2015).

In the last century, the increase in forest area in Portugal was marked by high human intervention, with forests now covering about 36% of the Portuguese national territory. In the first half of the century, afforestation happened as an effort to recover eroded soil, where large areas of maritime pine (*Pinus pinaster*), species native to the western Mediterranean region, were planted. However, after the 1970s, and in response to an increase in demand from the logging and paper industries, large areas were converted into non-native eucalyptus (*Eucalyptus globulus*) plantations, often at the expense of maritime pine (MAMAOT, 2013a; Reboredo and Pais, 2014), drastically changing the Portuguese forest composition (Jones et al., 2011;

Table 1
Key assumptions in Pathways A and B. For a full description of the pathways, see van Sluisveld et al. (2016).

Elements of Pathways	Pathway A	Pathway B
Common Agriculture Policy	Decrease in budget before disappearing	Budget remains more or less the same
Knowledge and innovation	Improve current developments: more efficiency	Broader knowledge base; more attention for business models
Technology	Hard technological solutions	Nature-friendly solutions
Consumers	More stringent standards for products	Extra attention for what is more than the standard
Chains	Global chains	Regional and local chains
Environmental policy	Stringent environmental policy and steering on innovation	Stringent environmental policy and steering on behaviour
Spatial planning	Separation of functions, land abandonment	Multifunctional land-use, fit in the landscape is more important
Markets	Global dynamics	Regional markets, decentralized societal debate
Sustainability approach	Sustainable intensification	Ecological intensification

Gonçalves and Pereira, 2015). Agro-forestry and forestry systems produce commodities such as cork and paper, which taken together generate a revenue that comprises 2% of the annual GDP and 10% of the national exports (ICNF, 2017).

These land-use and land cover change dynamics (e.g., changes in forest cover, agricultural abandonment and intensification of the agricultural land) have also shaped local biodiversity (Pereira et al., 2009). For instance, scrub encroachment associated with agricultural abandonment and forest plantation in agricultural land has been linked to declines in bird communities, particularly open farmland species (Moreira et al., 2012). Nonetheless, the increase in semi-natural vegetation resulting from agricultural abandonment has also favored the recovery of species previously impacted by the agriculture expansion (Pereira et al., 2009).

2.3. Projecting future land-use change in each pathway

We have characterized the land uses in Portugal into three main regimes: agriculture, forestry, and natural areas. Given the recent slowdown in urban area expansion and the fact that these areas only represent 4% of the national territory (Caetano et al., 2017), they were assumed to remain constant and thus excluded from the list of relevant land-use classes in this study. We further divided agriculture and forestry into intensive and extensive use of the land, resulting in five land-use classes: intensive agriculture, intensive forest, extensive agriculture, extensive forest and other natural (i.e., natural areas minus forests or agriculture areas). This segregation was due to the parameterization of the cSAR model as explained in section 2.4.

2.3.1. Data sources

We projected future changes in land-use until the year 2050, using a combination of datasets and tools, namely the CORINE Land Cover Map of 2012 (at 100 m resolution, EEA, 2016), the distribution map of forest tree species in Portugal (derived from the 2010 national forest inventory, Rosa et al., 2011), national statistics on agricultural areas (INE, 2011) and the Pathways narratives (see section 2.1). First, we created the baseline land-use map of 2010 by combining CORINE Land Cover (CLC) data for Portugal in 2012 with the forest species map produced by Rosa et al. (2011). We then reclassified the CLC classes into the five land-use classes of interest for this study (Table S1). Afterwards, using historical national statistics (1990–2010) from the National Forest Inventory (MAMAOT, 2013a) and the national Agricultural Census (INE, 2011), we determined the historical trends (i.e., % of land being converted per decade), which were then used and adapted to each scenario in order to produce the land-use maps for the year 2050 for Pathway 0, and the two sustainable pathways (Pathways A and B), respectively (see supplementary methods S1 for details).

2.3.2. Land-use transitions in Portugal under each pathway

To demonstrate analytically how such Pathways would impact species richness and composition across Portugal, we made a series of informed assumptions on future land-use trajectories. For the business-as-usual scenario (i.e., Pathway 0) we assumed that future land-use change will match the observed trends of the last 20 years (Table SM1, supplementary methods S1). Pathways A and B both have the same overall aim of reaching a sustainable society by 2050. However, they differ on the means to achieve such target, which has implications on the land-use transitions expected until 2050. For these two pathways, we modified the historical trends for the period 2010–2050 in order to fit the key assumptions of the storylines described above (section 2.1) while implementing, when appropriate, niche-innovations identified for each of the pathways (Gonçalves and Pereira, 2015). In particular, for Pathway A, both intensive agriculture and intensive forest were locked, meaning that the proportion of the area that they occupy in the country was assumed to not change from 2010 to 2050 (Table SM2, supplementary methods S1). Given the focus on technological improvements and the 'land-sparing' dimension of Pathway A, we expected that a significant increase in yield would lead to a sharp reduction of area needed to meet the necessary agriculture production. As a result, we assumed that the rate of loss in extensive agriculture would double compared to the historical trend, reflecting the abandonment of less productive and marginal agriculture areas, but maintaining the transitions rate to extensive forest and to other natural areas. In Pathway B, the area occupied by intensive forest was locked as well but we assumed a 50% reduction in the area of intensive agriculture by 2050 (Table SM3, supplementary methods S1), fitting the assumptions of this pathway. This area was assumed to be completely converted to extensive agriculture, representing the extensification of the landscape and an increase in multifunctional areas (i.e., 'land-sharing' dimension of Pathway B), which would be able to sustain agriculture production levels. We also locked the transition between extensive agriculture and extensive forest (e.g., no new pine plantations), and assumed a 50% reduction in the rate of extensive forest loss due to fire, since landscapes were assumed to be managed in order to be more fire resilient (Gonçalves and Pereira, 2015). Finally, we assumed that rewilding would be adopted as a land management approach, for both Pathways A and B, leading to a decrease in the rate of secondary succession, compared to the business-as-usual scenario.

2.3.3. Mapping future land-use change under each pathway

Land-use change is not uniformly distributed across Portugal, and the amount of land that is converted annually is a result of multiple drivers (e.g., socio-economic dynamics, presence of roads, topographic and climatic features) interacting simultaneously (Doorn and Bakker, 2007). The location in which this conversion takes place is often strongly spatially autocorrelated, i.e. newly created agricultural areas tends to occur closer to other agricultural areas rather than in areas undisturbed (Overmars et al., 2003; Rosa et al., 2013). Here the projected amount of land-use change was pre-determined based on the assumptions made for each Pathway, as explained in the previous section. Then, we used a simple spatially-explicit model to allocate the projected changes by 2050, assuming that transitions to a new land-use class (e.g., from intensive agriculture to extensive agriculture) would be more likely to occur closer to existing areas of the same land-use (i.e., extensive agriculture), thus expanding existing patches, rather than spontaneously creating new ones. To do so, we calculate the Euclidean distance of each pixel to each of the five land-use classes in 2010, and then iteratively selected the pixels to transition based on the minimum distance to a given land-use. As a result, we produced three new land-use maps for Portugal, each representing a different vision for 2050 (Pathways 0, A and B).

2.4. Effects of land-use change on biodiversity

Once the land-use maps for 2050 were created, we used the countryside species-area relationship (cSAR) (Pereira and Daily, 2006; Martins and Pereira, 2017) to assess the response of species richness to the projected changes in Pathways 0, A and B. In the countryside SAR, the proportion of species of a given functional group remaining in the landscape, after habitat conversion, will depend on the level of affinity of that species group to the human-modified habitats:

$$S_i = c_i \left(\sum_{j=1}^{n} h_{ij} A_j \right)^{z_i} \tag{1}$$

where S_i is the richness of each functional species group i, h_{ij} is the affinity of species group i to habitat j, A_j is the area cover by habitat j and n is the number of modified habitats types. The parameters c and z are constants that depend on the taxonomic group and sampling scheme respectively.

We used equation (1) to calculate alpha (10 km × 10 km UTM grid cells) and gamma (national) species richness of three different bird functional groups: forest species, farmland species and "other species" (i.e., species with affinity for other natural habitats, such as shrubland or grasslands) for the baseline and each of the three scenarios considered. The different functional group-specific parameters (i.e., c_i, z_i and h_{ij}, the habitat affinities) were derived from Martins et al. (2014), where the differential use of natural and human-modified habitats by different bird species groups in Portugal was assessed using this same method (Table S2). However, as the authors did not assess species responses to intensively used habitats, all affinities listed by Martins et al. (2014) were assumed to be for extensive landscapes. To estimate the habitat affinities for the intensively used habitats we used local studies across the Iberian Peninsula (see supplementary methods S2 and Table S3 for details).

The area of each land-use class (representing the different habitats) in each cell was calculated for the different land-use maps using ArcGIS 10.2 (ESRI, 2014), and used as an input in the cSAR. The total number of species in the landscape, S, was then given by the sum of species in each group ($S = \sum_{i=1}^{m} S_i$, where m is the number of species groups). Finally, we assessed the differences in species richness between the baseline (i.e., 2010) and the three projected Pathways for each functional species group as well as for the total species richness at the grid cell and national scales.

3. Results

3.1. Land-use change

We estimated that in the baseline (i.e., 2010) 60.9% of Portugal's territory (excluding urban areas) was under extensive use, while 20.8% of the area was being used intensively. The remaining area (18.3%) corresponded to natural areas that were neither forests nor agricultural areas and were not under any use (i.e., other natural, Table 2).

By 2050, and in the business-as-usual scenario (Pathway 0), we projected an increase in the area of both intensive and extensive forest, in the central and north-northeast part of Portugal (Fig. 1b, Table 2). Forest areas under intensive use are projected to increase as a consequence of the expansion of eucalyptus plantations, while the projected increase of extensive forest areas is mostly due to natural succession on abandoned farmland (see Table SM1 and supplementary methods S1 for

Table 2
Percentage of land (in %) occupied by the different land use classes in 2010 and by 2050 under the assumed scenarios (Pathways 0, A and B). Future trends of land-use change (in %) for the period 2010–2050 (in parentheses) under each scenario are also shown.

	Actual	Projected					
	2010	2050 (2010–2050)					
		Pathway 0		Pathway A		Pathway B	
Total area (%)							
Extensive Forest	26.5	32.9	(+24.3)	36.5	(+38.0)	30.4	(+14.8)
Intensive Forest	10.9	17.0	(+55.0)	10.9	(0)	11.0	(0)
Extensive Agriculture	34.5	29.4	(-14.7)	22.8	(-34.0)	38.4	(+11.5)
Intensive Agriculture	9.8	9.1	(-7.4)	9.8	(0)	4.9	(-50.0)
Other Natural	18.3	11.7	(-36.3)	20.0	(+9.7)	15.4	(-16.01)

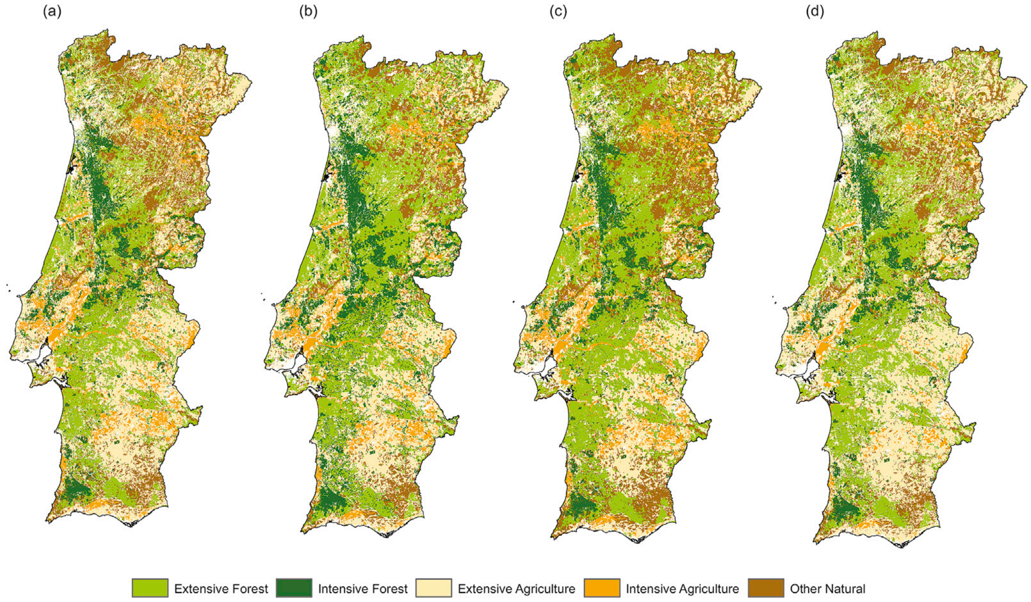

Fig. 1. Land-use maps of Portugal in the baseline (**a**; 2010), and in Pathways 0 (**b**), A (**c**) and B (**d**) in 2050.

details). Areas devoted to extensive agricultural production are projected to decrease by 14.7% (Table 1), according to historical trends, based on the storyline assumptions. In the southeast and northeast part of Portugal, such a decrease is projected to be a result of land abandonment (i.e., conversion to other natural areas) and intensification of the agricultural areas, while in the center and northwest of the country agriculture areas are mostly converted to extensive forest areas (e.g., new pine plantations). By 2050, more natural areas are being actively converted to forest than are being created by agricultural abandonment or by fire events, leading to an overall reduction of the country's other natural areas (11.7% in 2050 *vs* 18.3% in 2010, Table 1 and Table SM1).

Given the focus on technological improvements and the 'land-sparing' dimension of Pathway A, intensive agricultural areas remain constant, as a result of our assumptions, but a strong reduction in the area devoted to extensive agriculture in the north- and northeast of Portugal is projected. From 34.5% in 2010, extensive agriculture reduces to 22.8% in 2050 as a result of agricultural land abandonment, and conversion to extensive forest (e.g., new pine plantations, see Table 1 and Table SM2 for details). Moreover, in Pathway A we projected an increase in extensive forest and other natural areas, which taken together would represent 56.5% of the non-urban area of the country by 2050.

In Pathway B, and following the behavioral changes associated with the underlying scenario, the overall area of agriculture remains relatively stable compared to 2010 (43.4% in 2050 *vs* 44.3% in 2010, Table 1 and Table SM3). However, the high rate of extensification of agricultural areas projected to occur (i.e., the key assumption of a loss of 50% of all intensive agriculture areas) as expected by the 'land-sharing' approach of Pathway B, lead to an increase in the country's multifunctional areas, particularly in the central and southeast part of Portugal. From 34.5% in 2010, it increases to 38.4% in 2050. Extensive forest and other natural areas are also projected to increase, representing 45.7% of the non-urban area of the country by 2050.

3.2. Biodiversity change

In Pathway A and Pathway B, on average across all 10 km $\times$ 10 km cells, the total alpha diversity is projected to increase, whereas in Pathway 0 it is projected to decrease (Fig. 2, Table S4). In all scenarios, species groups' responses to land-use change vary in intensity and even in direction across different regions of Portugal (Fig. 3). For instance, in Pathway 0, both alpha and gamma diversity of farmland species and other species are projected to decrease, while forest species richness is projected to increase. In the north of Portugal, alpha diversity is projected to increase, due to agricultural land abandonment leading to the expansion of both natural and extensive forest areas, favoring both forest and other bird species (Fig. 3b, d). In contrast, as more area is converted to forest (intensive and extensive) species richness of other birds decreases, particularly across the west and center of Portugal (Fig. 3d), thus leading to a reduction, on average, in the levels of alpha diversity of other species (Fig. 2d). Farmland species loss seems to be more equally distributed across the country, as agriculture areas are projected to decrease in all parts of Portugal (Fig. 3c).

The technological improvement scenario (i.e., Pathway A) results in the highest rates of biodiversity change (i.e., +0.73 *sp.* s.d. = 0.43 at the local scale and +1.54 *sp.* at the national scale; Table S4). In this scenario, both the forest and other species richness are projected to increase, while farmland species richness is projected to decrease (Fig. 2, Table S4). Here, changes in both forest species and farmland species occur in all regions of Portugal (Fig. 3b and c), as the loss of agricultural areas leads to

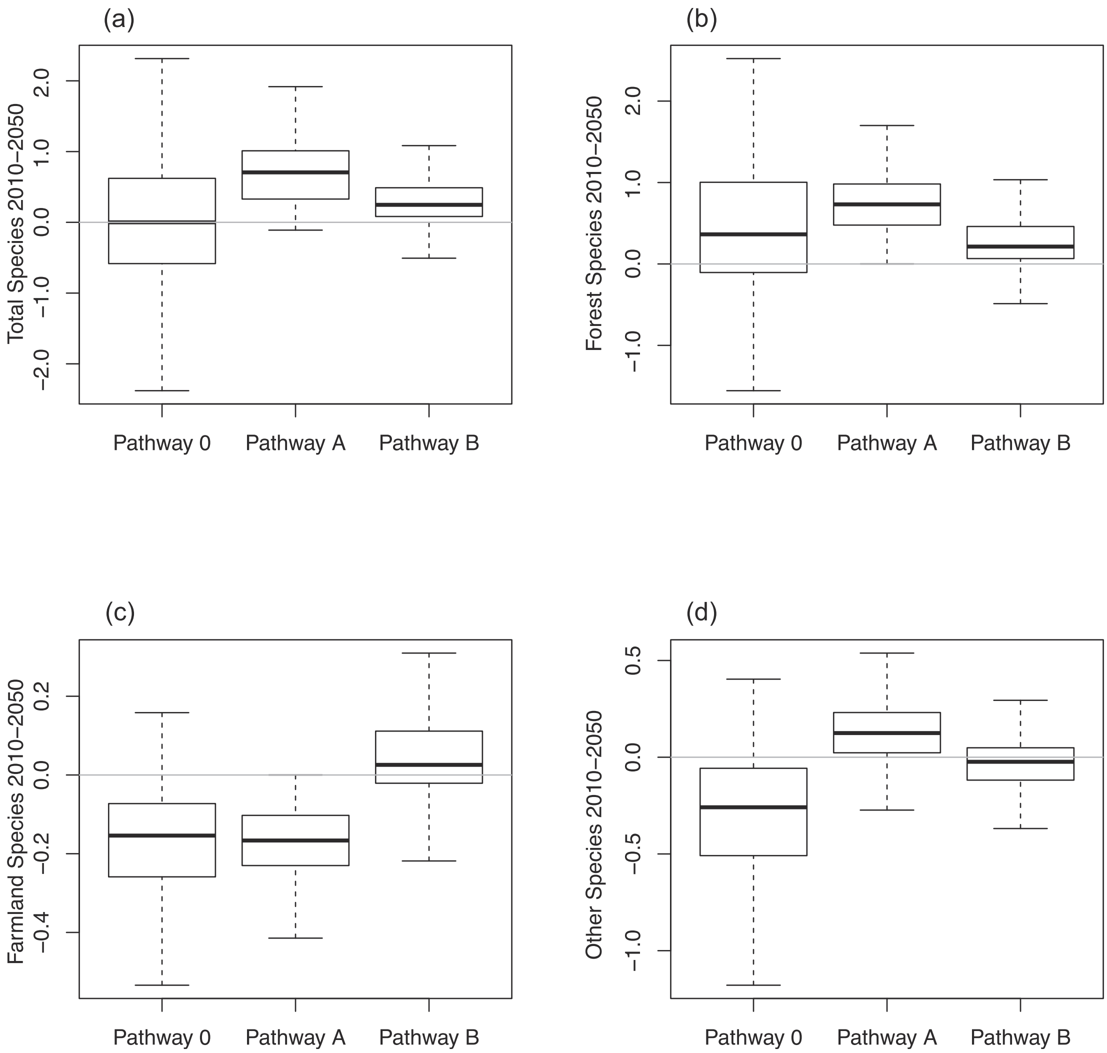

Fig. 2. Boxplots of the change in species richness between 2010 and 2050 in Pathways 0, A, and B across 10 × 10 km grid-cells: Total species (**a**), forest species (**b**), farmland species (**c**) and other species (**d**). From left to right: Pathway 0, Pathway A, and Pathway B. Unit: number of bird species. The thick horizontal line in the middle of each box represents the median of the data, while the bottom and top of each box represent the 25th and 75th percentiles, respectively.

an enlargement of both natural areas and extensive forest areas. Consequently, other species' richness increase, particularly in the east of Portugal (Fig. 3d), as natural areas expand.

The changes in alpha species richness in Pathway B are more moderate across the entire country (i.e., +0.33 *sp.* s.d. = 0.30 at the local scale and +0.63 *sp.* at the national scale; Table S4), with farmland species richness projected to increase, and both forest species richness and the richness of other species projected to decrease (Fig. 2). In Pathway B, the gain of forest species is centered in the northeast part of the country (Fig. 3b), where most extensive forest is projected to expand as a result of natural succession. The richness of farmland species is projected to improve, as multifunctionality, particularly in the central and southeast part of Portugal, increases both the area and niches available to these species. Nonetheless, farmland species loss still occurs in this scenario, but limited to the north part of Portugal (Fig. 3c), where some agricultural land abandonment is still projected to occur (Figs. 1 and 3).

4. Discussion

Projecting the future of landscapes under a range of scenarios is a key step towards making management decisions that are likely to promote biodiversity and ecosystem services (van Vuuren et al., 2012; Rosa et al., 2017). As well as a useful tool for policy- and decision-makers to predict the impact of their actions prior to their implementation (Ferrier et al., 2016) under 'what-if' situations involving a key set of assumptions (Nicholson et al., 2019). Yet, studies projecting the future of biodiversity

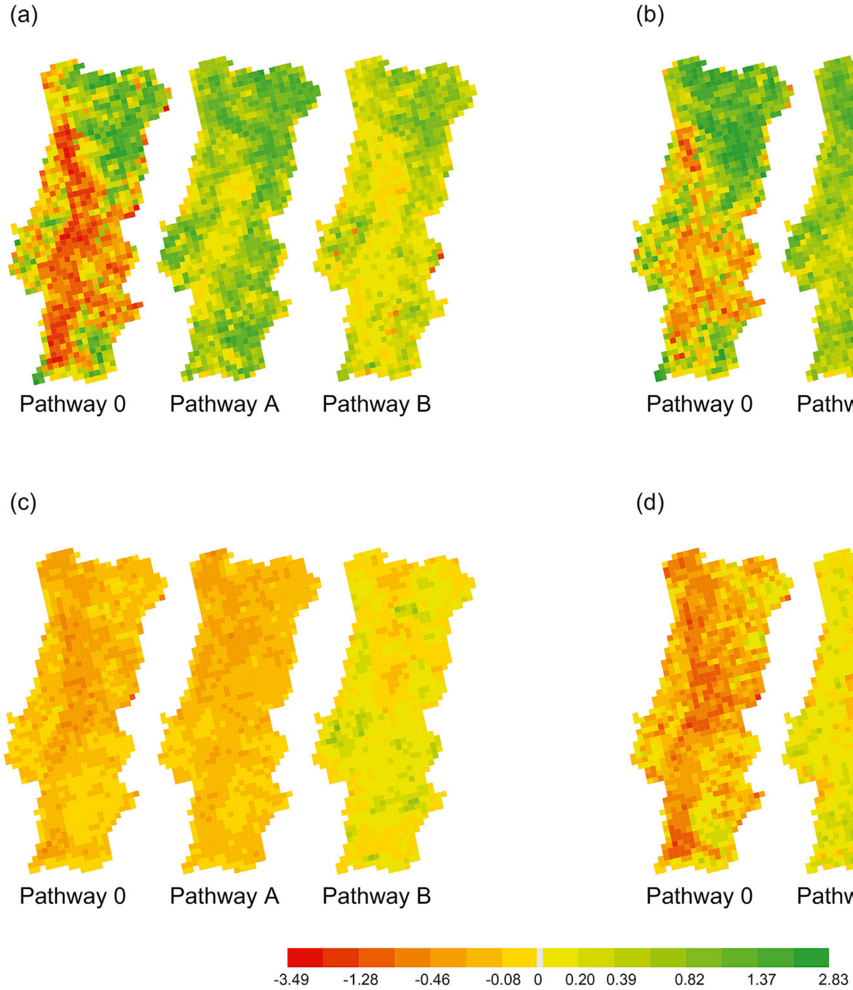

Fig. 3. Change in alpha species richness of the different species groups between the baseline 2010 and the different pathways in 2050: Total species (**a**), forest species (**b**), farmland species (**c**) and other species (**d**). Unit: number of bird species.

within human-dominated landscapes tend to neglect that biodiversity loss is not random with regard to identity and functional performance of the species (Hillebrand et al., 2018).

Our scenario analysis highlights that while multiple positive futures for biodiversity may be envisioned, they would lead to differential impacts on biodiversity depending on the type of transformational changes and the regional socio-economic context. For instance, in the technical component substitution scenario (Pathway A), species associated with "natural areas" (e.g., forest species and other species) were projected to expand as more habitat becomes available, as a result of the increase in farmland abandonment and consequently natural habitats. It has been argued that the current trend of farmland abandonment in Europe (Levers et al., 2015; Schultz et al., 2015) should be welcomed by the conservation community as an opportunity to improve habitat condition for species (Queiroz et al., 2014) and as an opportunity for rewilding (Navarro and Pereira, 2012). However, in the technological change scenario forest species increase at the expense of farmland species. Under these conditions, farmland species that rely on open habitats would likely see their range restricted to the more intensively used agricultural areas. Our results, although linked to the assumptions of the pathways, agree with previous studies highlighting the conservation value of farmland habitats (Moreira and Russo, 2007; Brambilla et al., 2010; Moreira et al., 2012), especially in the Mediterranean basin, a region where a long-term and complex history of human exploitation has largely shaped its landscape and associated fauna (Blondel, 2006; Blondel et al., 2010; Navarro and Pereira, 2012). For instance, a decrease in the extent of open/farmland landscapes is thought to affect negatively the black-bellied sandgrouse (*Pterocles orientalis*), little bustard (*Tetrax tetrax*) and Cabrera's vole (*Microtus cabrerae*) (Moreira and Russo, 2007), three Mediterranean species that are assessed respectively as endangered, vulnerable, and near threatened by the IUCN.

On the other hand, the broader regime transformation scenario (Pathway B) suggests that a multifunctional landscape, where wildlife-friendly farming methods and semi-natural environments function synergistically, would be able to sustain species richness by improving habitat quality, as well as support a higher diversity of species. However, results from the cSAR model show that this scenario would clearly favor farmland species over other species groups, a trend that is not present in the two other scenarios. The differences observed between the grid cell and national level species responses to land-use change were expected according to Martins and Pereira (2017). That is, at a very small scale, the habitats are homogenous and one either considers species entirely within native or entirely within a human-modified habitat. In contrast, at larger scales, any sampling unit is a mixture of both habitats and the effect of land-use change on the SAR decreases. While our study focused only on birds, as a well-studied group of organisms that tends to rapidly respond to environmental change (BirdLife International, 2013), a broader analysis of diversity change (i.e., including other species groups) is expected to show similar directional changes, as species responses to land-use change are based on their sensitivity to change and habitat preferences. For instance, a meta-analysis by Acevedo-Charry and Aide (2019) showed that several vertebrate groups were equally affected by tropical secondary forest succession, with species richness increasing, but forest specialists decreasing across all taxons. It is essential to note that while most species may persist in the landscape even after significant land-use changes, large variations may occur in the relative abundance of species, a variable that is not accounted for in the countryside SAR model.

Conservation efforts should be implemented to safeguard most impacted species and/or strategies to maintain their habitat requirements within the landscape, thus minimizing losses. For instance, the impact of agricultural abandonment on farmland species observed in Pathway A could be mitigated by maintaining patches of extensive agriculture, or by reintroducing large herbivores to limit secondary succession (while restoring trophic complexity), and/or restoring stochastic disturbance regimes (Navarro et al., 2015; Svenning et al., 2016; Perino et al., 2019). Although rewilding was considered as a strategy in both pathways, the restoration of these ecological processes, and their likely impact on the distribution of habitats could not be accounted for using the cSAR approach. Additionally, the impact on forest and other non-farmland species could be lessened by expanding natural forests (Proença et al., 2010). Overall, losses could be avoided or mitigated by expanding the network of protected areas in the country, as most of the species loss projected in our study, particularly in the center and southeast (Alentejo and Algarve), will occur outside of protected areas (UNEP-WCMC, 2017) and often inside Key Biodiversity Areas (KBAs) (BirdLife International, 2019).

Although there are different management strategies for preventing further loss of biodiversity, it is also clearly not preferable or even possible to implement the same measures everywhere. In line with much of the recent discussion around the "land-sparing *versus* land-sharing" framework (e.g., Fischer et al. 2014; Kremen, 2015), we argue that both approaches should not necessarily be mutually exclusive at larger scales since their potential impacts on biodiversity are context-dependent. For example, in Portugal, land-sparing strategies present some opportunities, as there is scope to increase yields in existing agriculture areas, while the abandonment of marginal and less productive lands would present an opportunity for rewilding and conservation (Merckx and Pereira, 2015). However, such strategy is likely to mainly benefit biodiversity in the center and north of Portugal, regions already undergoing extensive farmland abandonment (Pereira et al., 2009). In contrast, most of the south of Portugal is characterized by *Montados*, a well-established agro-forestry system that supports high levels of biodiversity and ecosystem services (i.e., land-sharing strategy) and plays an important role in the Portuguese economy (Pinto-Correia et al., 2011). Our results suggest that in countries with heterogenous ecosystems (such as our case study), both the national and local landscape context needs to be considered in the development of policies promoting a given conservation measure. Overall, it is likely that the relative merit of each approach to safeguard species will be context-dependent, shifting based on the local conservation, socio-economic goals, history of land-use change and cultural practices (Kremen, 2015; Salles et al., 2017). For instance, a similar analysis across the Netherlands showed that land-sharing strategies alone seem to produce the strongest biodiversity benefits across the country (i.e., both at the local and national scale), since the Dutch landscape is not only very homogeneous but has also been heavily intensified in the past (Zwartkruis et al., 2016).

While each country has its own specific opportunities and challenges, indicating the importance of national policies, these need to be formulated within the international context in order to reach common targets and goals (e.g., Common Agriculture Policy, European Union biodiversity strategy, current and post-2020 global biodiversity framework of the CBD). Although our scenario-based study covers only one country and taxon, involving a key set of assumptions specific to our analysis, there are important insights that can be drawn from it to a wider context. For instance, the different land management options explored here could be used to make scenarios of more biodiversity-friendly land-use decisions, and assess their impacts on the diversity of landscapes in other countries. Furthermore, as policy- and decision-makers operate on limited budgets, our spatially-explicit and cross-scale approach could be used to support prioritization exercises and conservation actions at larger scales, under different sets of assumptions. For example, the modeling framework could help identify regions where changing land-use policies could have the largest benefits on biodiversity, and assess which areas should focus on agricultural production and which areas are more suitable for conserving nature. Additionally, by combining national-scale and cross-country analyses such an approach could potentially help countries coordinate efforts, by considering cross-border socio-economic relationships and remote responsibility, and thus promote sustainability while maintaining minimal impacts on biodiversity (Marques et al., 2019).

When interpreting our results, it is important to consider the limitations of our approach. We quantified changes in biodiversity based on changes in habitat area only (strongly influenced by the pathways assumptions) and without considering potential changes in fragmentation and habitat configuration, which can influence habitat use (Fahrig and Triantis, 2013). We did so because while our land-use model is spatially explicit, it is not designed to project land-use at the scale of habitat patches. Moreover, we did not include other drivers of change, such as climate change, despite it being known to influence and often exacerbate the impact that land-use change has on biodiversity (e.g., Visconti et al., 2016). For example, species that are disproportionally sensitive to land-use change (e.g., narrow-ranged species) are more likely to be sensible to climate change as well (Frishkoff et al., 2016). Further, land-use change may influence the ability of both resident and migratory bird species to disperse in response to climate change (Lemoine et al., 2007). Currently, there is insufficient information to account properly for these interactions, in part due to the very different scales at which land-use and climate processes operate (but see Newbold, 2018). While both scenarios presented here project a substantial reduction of greenhouse gas emissions by 2050 (van Sluisveld et al., 2016), thus mitigating the effect of climate change, some climate change is still expected to occur. As a result, our estimates can be considered conservative.

It is important to note also, as for any other SAR approach, the cSAR does not estimate the biodiversity that will change between 2010 and 2050 (i.e., within a specific time frame) rather the approach estimates the number of species which are expected to persist or become extinct over the long term, as a consequence of the land-use conditions observed or predicted by 2050. Finally, while theoretical frameworks that measure changes in species richness, like the cSAR, are essential to understand the nuance of changes in species diversity, and species composition, under different scenarios of change, future studies should aim for more integrative approaches. Thus, capturing in one model, other key attributes such as changes in abundance, and community structure that may lead to further biodiversity changes.

Ultimately, species diversity is key for a rich and diverse set of ecosystem services (Mace et al., 2012), therefore it is essential to aim for a diversity of habitats in order to sustain higher levels of biodiversity, while ensuring the benefits for people that ecosystems provide. Sustained by our analysis, we argue that any attempts at improving national biodiversity levels (in this case species diversity), for instance to accommodate for international agreements and targets, through conservation or management actions, should consider regional differences not only in terms of species and ecosystems present, but also socio-economic dynamics that might be impacted by such actions. Furthermore, people's preferences for compositional aspects of biodiversity can be critical in choosing the appropriate land-use policies.

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Appendix A. Supplementary data

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