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Integrating ecosystem services within spatial biodiversity conservation prioritization in the Alps

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ABSTRACT

As anthropogenic degradation of biodiversity and ecosystems increases, so does the potential threat to the supply of ecosystem services, a key contribution of nature to people. Biodiversity has often been used in spatial conservation planning and has been regarded as one among multiple services delivered by ecosystems. Hence, biodiversity conservation planning should be integrated in a framework of prioritizing services in order to inform decision-making. Here, we propose a prioritization approach based on scenarios maximising both the provision of ecosystem services and the conservation of biodiversity hotspots. Different weighting scenarios for the α-diversity in four taxonomic groups and 10 mapped ecosystem services were used to simulate varying priorities of policymakers in a mountain region. Our results illustrate how increasing priorities to ecosystem services can be disadvantageous to biodiversity. Moreover, the analysis to identify priority areas that best compromise the conservation of α-diversity and ecosystem services are predominantly not located within the current protected area network. Our analyses stress the need for an appropriate weighting of biodiversity within decision making that seek to integrate multiple ecosystem services. Our study paves the way toward further integration of multiple biodiversity groups and components, ecosystem services and various socio-economic scenarios, ultimately fuelling the development of more informed, evidence-based spatial planning decisions for conservation.

1. Introduction

Humans are degrading ecosystems on which our societies highly depend, leading to irreversible biodiversity losses, with extinction rates 100 times greater over the last century than recorded in the fossil records (IPBES, 2018) and further losses predicted in the future (Braat et al., 2008; Vellend et al., 2017). Biodiversity represents the living part of our natural capital and plays a crucial role in the functioning of ecosystems (MEA, 2005; Diaz et al., 2006; Balvanera et al., 2006; Harrison et al., 2014). Compared to previous action plans for biodiversity conservation, the Aichi biodiversity targets (CBD, 2010), the post-2020 Global Biodiversity Framework (CBD/WG2020/2/3, 2020), and the United Nations' Sustainable Development Goals include the concept of ecosystem services (ES) in their strategies (IPBES, 2018). ES are usually defined as the benefits or contributions people obtain from ecosystems (MEA, 2005; IPBES, 2018). This definition emphasizes the various gains supplied by functioning ecosystems (De Groot et al., 2010b; Haines-Young and Potschin, 2010), comprising provision (e.g. wood, food, clean water), regulation (e.g. pollination, flood prevention, climatic regulation), and cultural services (e.g. recreation, cognitive

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development). Land-use changes and environmental pressures induce modifications in biodiversity and ecosystem functions, leading to loss of ES (Costanza et al., 1997; Daily, 1997; Braat et al., 2008), which could then affect human societies (IPBES, 2018). There is thus an increasing need to develop plans that sustain ecosystems and the services they supply (Costanza et al., 2017).

A general decline in the quality of public goods and non-marketable services has been associated to inefficient planning and management of common resources (Lant et al., 2008; Burkhard and Maes, 2017). The valuation of ES in policies is a starting point to highlight nature conservation benefits, giving an anthropogenic justification for preserving biodiversity (Reid et al., 2006). There are various types of values, defined as “the contribution of an action or object to user-specified goals, objectives, or conditions” (MEA, 2005). Recently, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) emphasized the importance of a pluralistic valuation approach comprising biophysical, sociocultural and economical components (Pascual et al., 2017; Gunton et al., 2017). Economic valuation of ES has the advantage of being comparable with the value of other consumptive goods, enabling the assessment of the socio-economic costs of reduced ES due to biodiversity loss (e.g. Cost of Political Inaction project; Braat et al., 2008). Braat et al. (2008) estimated the loss of well-being due to the reduction of biodiversity and ES by 2050 at ca. €14 trillion (7% of the projected global GDP). These results show the importance of ES for the regional economy, especially for alpine regions which are highly dependent on the supply of multiple services (Grêt-Regamey et al., 2008b; Häyhä et al., 2015; Rewitzer et al., 2017), and stimulated initiatives to quantify and value ES in order to guide decisions on complex public issues (e.g. in Europe; Maes et al. 2013).

Mountains represent key regions for preserving biodiversity and functioning ES, which have further benefits for lower elevation areas (Becker et al., 2007; Martín-López et al., 2019). Mountains represent a quarter of the Earth's surface (The Panos Institute, 2002), shelter many of the world’s principal biomes (Grêt-Regamey et al., 2012; Payne et al., 2017; Martín-López et al., 2019), and many ES are dependent on their development (e.g. water regulation: Viviroli et al., 2007; timber/agriculture/animal products: Locatelli et al., 2017; recreation activities: Beza, 2010, Rewitzer et al., 2017). Yet, mountain ecosystems are under multiple threats and pressures (e.g. climate and land use change; Bugmann et al., 2007; Beniston, 2016; Palomo, 2017), making it important to assess their fate and ensure their preservation and functioning (Brunner and Grêt-Regamey, 2016, Egan and Price, 2017).

Conservation actions for biodiversity protection and ES maintenance have however a cost, and strategies are required to invest limited resources efficiently (Margules and Pressey, 2000, Naidoo et al., 2008). Decision support tools, such as Spatial Conservation Prioritization (Moilanen et al., 2011), can be used to identify priority areas that are important for the protection of biodiversity and other ecosystem features (Snäll et al., 2016; Vincent et al., 2019). Until now, the majority of priority areas for conservation were based on habitats and/or species of interest at particular locations without attempting to include biodiversity models in the analysis, e.g. through predictive models (Tulloch et al., 2016). At the same time, the decrease in ES supply and the recognition of their importance to human well-being have raised growing interest for their additional integration into spatial conservation planning (IPBES, 2018). The goal of such analyses is to spatially optimize the provisioning of ES while ensuring biodiversity protection (Chan et al., 2006; Pascual et al., 2016).

A small but increasing number of examples exist that combine ES and biodiversity conservation in the same spatial prioritization framework at a coarse spatial scale (Luck et al., 2009, 2012; Durán et al., 2014; Schröter and Remme, 2016; Kukkala and Moilanen, 2017). For instance, Maes et al. (2012) proposed an approach between the diversity and abundance of tree species in relation to ES at the European scale and found that habitats like Natura 2000 sites are important for supporting both biodiversity and ES components. Castro et al. (2015) found similar results at a local scale where ES were supported in protected areas (PAs) where biodiversity was high. Simultaneously protecting biodiversity and ES can occur when they are closely linked (e.g. wealth and productivity; Costanza et al., 2007), but in some cases, intense human activity behind ES development can damage biodiversity (Tolvanen and Kangas, 2016). Priorities for ES and biodiversity can be combined to propose new PAs that optimize both (Xu et al., 2017). Although mountains represent key areas for ES for the greater landscape (Grêt-Regamey et al., 2007), we are not aware of any study combining ES and biodiversity in the same Spatial Conservation Prioritization framework in a mountain landscape.

Here, we propose a Spatial Conservation Prioritization framework combining both predicted α-level biodiversity (hereafter simply ‘biodiversity’) through the predicted presence-absence of species, with different weightings according to their conservation status (i.e. weighted richness), in four taxonomic groups (as used in Vincent et al., 2019) and the Total Economic Value (TEV) of ten ES in a mountain region of conservation interest in the Swiss Alps. We compiled an ecosystem map and used it to identify ES in the study area and applied several data and valuation methods to assign them economic values. The Zonation software was used to integrate ES and biodiversity predictions into the same Spatial Conservation Prioritization analysis (Lehtomäki and Moilanen, 2013). We gradually increased the weight given to ES compared to biodiversity in the Spatial Conservation Prioritization to determine whether an increased preference of stakeholders to prioritize ES would be advantageous or detrimental to the biodiversity of the taxonomic groups considered. For this, we compared the performances and spatial overlap between prioritization solutions, within and outside current protected areas, to assess whether the integration of ES could change conservation plans based on biodiversity only, and whether conflicts could be identified between ES hotspots and biodiversity hotspots. Specifically, we ask the following questions:

- Would the areas contributing most to preserve both biodiversity and ES coincide spatially, as suggested from work at the European scale (Maes et al., 2012)?
- How could conflicting priorities of these two components affect spatial solutions?
- Would current protected areas contribute to conserving suitable habitats for both biodiversity and ES, as suggested in other regions (e.g. semi-arid ecosystems; Castro et al., 2015)?

We further look at the distribution of the identified spatial priorities along the elevation gradient, as the latter drives all main environmental and human activities in the study area and therefore can influence where new protected areas could be created (i.e. easier in high-elevation areas than in the more crowded lowlands). As several of our ES are related to forests, but biodiversity in the taxa included here tend to occur more in open habitats, we expect a certain level of mismatch to be found when giving priority to one element over the other. Furthermore, as the current protected areas were often set up with the aim of safeguarding some specific species and habitats, we expect them overall to favour α-diversity more than ES (at least more than the provisioning ES; e.g. agriculture; Joppa and Pfaff, 2009). From previous studies on the distribution of the four taxonomic groups considered here (Grossenbacher, 1988; Dubuis et al., 2011; D'Amen et al., 2018; Pittet, 2017), and due to the dominance of plants among species, species richness is expected to be highest at mid-elevations (1000–1800 m). Expectations are more difficult to draw for ES, but higher values could also be expected at mid-elevations where mixed forest occurs which tend to increase ES value (Schuler et al. 2017) and where recreation ES are also often observed (Lavorel et al., 2020).

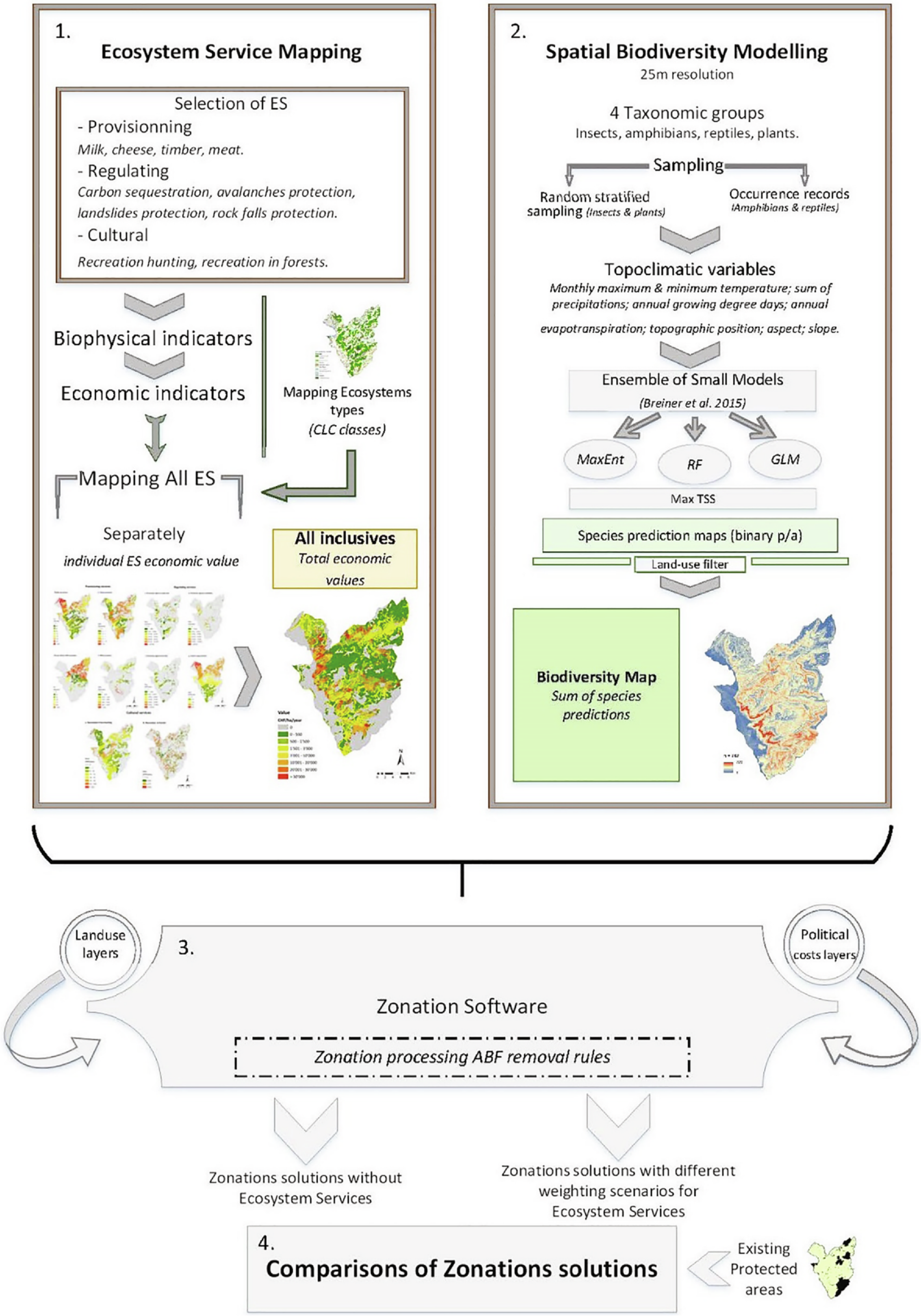

Fig. 1. Conceptual framework representing the different analytical steps followed in this case study (expanded from Vincent et al., 2019). **1.** Mapping the monetary values of 10 ES. **2.** Spatial modelling of biodiversity based on 767 species in four taxonomic groups. **3.** The outputs from steps 1&2 are used in spatial prioritization analyses in the Zonation software, additionally considering land use and political costs. **4.** Comparisons of the Zonation Spatial Conservation Prioritization solutions with different weights for biodiversity and ES respectively, within and outside existing protected areas. The small maps in boxes 1 and 2 can be found in a larger format in Appendix C Figs.S1-S4.

2. Methods

2.1. General framework

We developed a Spatial Conservation Prioritization framework in the Zonation software (Lehtomäki and Moilanen, 2013) for a mountain area of special conservation interest in the Swiss Alps, comprising four main steps (Fig. 1). First, we mapped ecosystems in the study area and derived a new map of 10 ES with economic values assigned. Second, we used existing occurrences of 767 species in four taxonomic groups and environmental data to model their distributions and added the predictions as biodiversity inputs in further analyses based on topo-climatic variables and a land use filter. Third, we ran a series of Spatial Conservation Prioritization analyses with different priority scenarios for biodiversity and ES with the mapped outputs from the previous two steps, together with maps of land use and political costs (from Vincent et al., 2019). Fourth, we compared the outcomes (i.e. “solutions”) of the different Spatial Conservation Prioritization scenarios to each other and to the existing network of protected areas (Fig. 1).

2.2. Study area

The study area is located in the Western Swiss Alps (6°60′ to 7°10′ E; 46°10′ to 46°30′ N; hereafter *Vaud Alps*). It covers an area of ca. 700 km^2, with elevations ranging from 1300 to 3120 m. Various ecosystems are present, comprising different types of forests, grasslands/meadows, wetlands and agricultural lands (Fig. 2). The region benefits from great tourism assets due to its rich natural landscapes and cultural heritage. More than 60% of the area is considered important for biodiversity and ecosystem conservation, with 18% of the landscape designated as a “Strict Nature Reserve” (IUCN Category Ia) or a “Habitat/Species Management Area” (IUCN Category IV). The region is also a WWF priority area for conservation (WWF, 2015) and a special area for interdisciplinary research at the University of Lausanne, supported by a geoportal containing scientific metadata and information (http://rechalp.unil.ch).

2.3. Mapping the economic values of ecosystem services

A subset of 10 ES recognized by the Common International Classification of Ecosystem Services (CICES) typology (Haines-Young and Potschin, 2012) were selected to be quantified and valued. The most frequently used ES were identified from the literature (Schmidt et al., 2016; Grêt-Regamey et al., 2008a), from which ten locally quantifiable services were selected: four provisioning services (*timber, meat, milk,* and *cheese ‘Etivaz AOP’*), four regulating services (*carbon sequestration, protection against avalanches, landslides* and *rock falls*) and two cultural services (*recreation in forests* and *hunting*) (Table 1). Additional unmapped ES, that were not included in this study due to the low quality of the data, are described in Appendix A (Table A3). For milk and cheese provision, data were available for each commune (i.e. administrative division) within the study area. For timber provision and carbon sequestration, data were available for each forest district. Hunting ES (i.e. *meat provision and recreation*) were mapped for each wildlife area, defined as the spatial unit for hunting statistics (Schmidt, 2000). Recreation in the forest was identified by the presence of forest attributes that were appreciated by people, such as hiking trails and watersheds. The heterogeneity of recreation was represented by combining these attributes, creating four levels of recreation (OFEV et WSL, 2013).

Biophysical indicators were used as proxies to quantify the goods and services provided by ecosystems (Czúcz and Arany, 2015). Some of the indicators (timber provision, meat provision, rock falls, carbon sequestration) used in this study were taken from a list proposed by the Swiss Federal Office for the Environment (Staub et al., 2011). Provisioning ES were quantified based on the quantity produced or harvested (see Appendix B, part 1). Carbon sequestration was quantified using a formula adapted from Häyhä et al. (2015), which translates wood increment into kilograms of CO_2 sequestered by trees per hectare per year (i.e., we did not include carbon sequestration by wetlands). For this, we

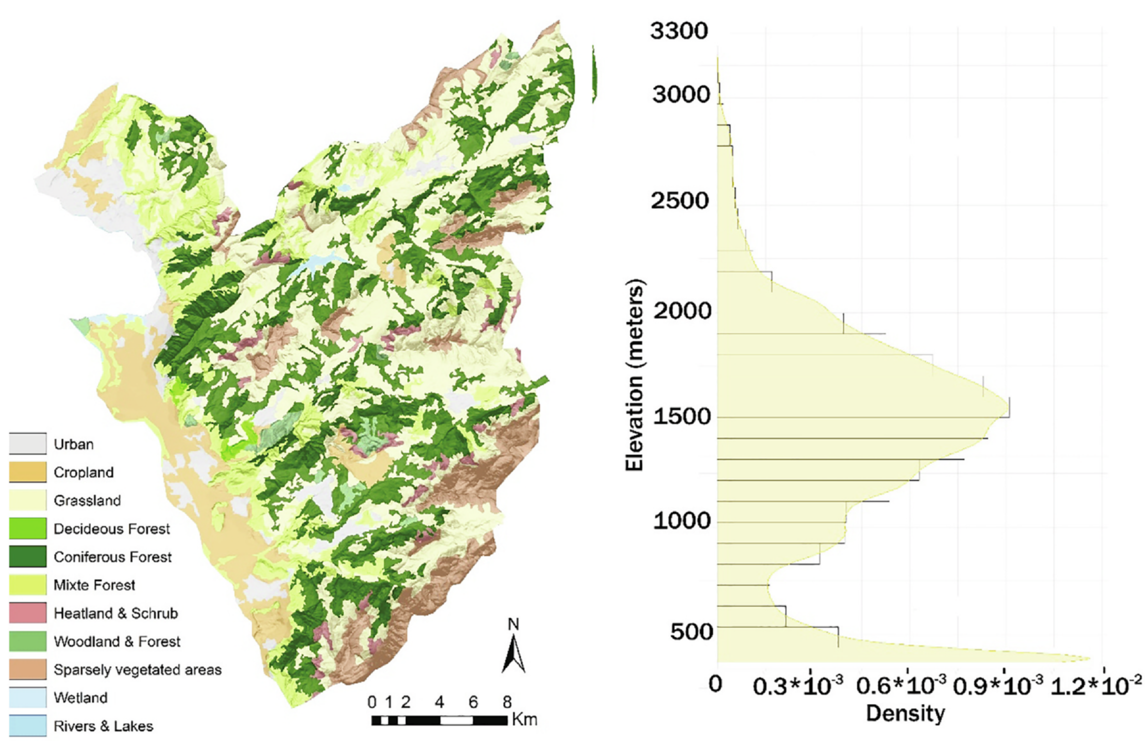

Fig. 2. Map of ecosystem types for the Vaud Alps study area. Ecosystem types were mapped according to their correspondence with Corine-Land-Cover classes (CLC), following a typology proposed by the Mapping and Assessment of Ecosystems and their Services (MAES) initiative. On the right the distribution of the raster cells (25x25m) according to elevation (m) in the Vaud Alps.

Table 1
Subset of ES considered in this study, classified according to the CICES typology (Haines-Young and Potschin, 2012), with corresponding biophysical and economic indicators used for the quantification and valuation. Units used for biophysical quantification and the valuation method chosen for each ES is also specified, as well as the ecosystem type that provides each service.

Category of Service	CICES Division	CICES Group	CICES Class	Class Type	Biophysical Indicator	Unit	Economic indicator	Ecosystem	Resolution	Valuation method
Provisioning	Nutrition	Biomass	Reared animals and their output	**Milk production**	Milk production	Kg	Price of milk	Grasslands	Commune	Market price
				Cheese Etivaz AOP provision	Cheese production	Kg	Price of Etivaz AOP	Grasslands	Commune	Market price
			Wild animals and their output	**Meat from game**	Meat from wild animals	Head	Price of meat	Forests	Wildlife area	Market price
	Materials	Biomass	Fibres and materials from plants	**Timber provision**	Timber harvested	m3/ha	Market price of timber	Forests	Forest district	Market price
Regulating	Mediation of flows	Mass flows	Mass stabilisation and control of erosion	**Protection against avalanches**	Protective forest & risk zones	Ha	Infrastructures value	Forests	Study area	Avoided damage costs
				Protection against rock falls	Protective forest & risk zones	Ha	Infrastructures value	Forests	Study area	Avoided damage costs
				Protection against landslides	Protective forest & risk zones	Ha	Infrastructures value	Forests	Study area	Avoided damage costs
	Maintenance of biological conditions	Climate regulation	Reduction of greenhouse gas concentrations	**Carbon sequestration**	Annual wood increment	m3/ha	Market price of carbon	Forests	Forest district	Market price
Cultural	Physical and intellectual interactions	Physical and experimental interactions	Physical use of landscape	**Hunting**	Number of animals harvested	Head	Price of licences	Forests	Wildlife area	Revealed preference
				Recreation in forest	People's preferences for forest attributes		Willingness to pay (WaMos 2 study)	Forests	Study area	Expenditure method

used data from the Swiss National Forest Inventory (NFI), which provides hardwood and conifer growth data for the same years by forest district (in m^3/ha/year; Hofer et al., 2010; FOEN, 2020). The protective role of forests against avalanches, landslides and rock falls was quantified based on roads and buildings considered as protected by those forests. Additional details about the quantification of regulating services are available in Appendix B, part 2. Recreation from hunting activity was quantified using the same set of data as for game provision (i.e. the number of animals harvested by hunters). Recreation in forests was quantified based on people's preferences for forest attributes, revealed by the second Switzerland-wide survey on Socio-cultural Monitoring (WaMos 2) carried out in 2010 (OFEV & WSL, 2013). Detailed quantification and valuation of cultural ES are available in Appendix B, part 3. A map of ecosystem types was finally created in ArcGIS 10.2 (resolution 100 m × 100 m), based on the recent typology of ecosystems (Maes et al., 2013) (Fig. 2), which distinguishes 11 main types, built from the European Union Nature Information System (EUNIS) habitat classification (Davies et al., 2004) and corresponding Corine-Land-Cover (CLC) classes (see Appendix A, Table A1).

A range of monetary and non-monetary valuation approaches to ES have been described and are listed in Appendix A (Table A2). The choice of the valuation technique depends on the type of service to value, as well as the quantity and quality of data available. We used different methods to estimate the economic values of selected ES. The market price method (Pascual et al., 2010) was used for provisioning ES, using the current market price per unit of marketed goods. Hydrogeological protection services were valued by using the avoided damage costs method (Barth and Döll, 2016; Brander and Crossman, 2017). To value carbon sequestration, the Social Cost of Carbon (SCC) of 40.8 CHF/ton of CO_2 was used (Appendix B, Part 2). Valuation methods based on people's preferences were used to assess people's minimum willingness to pay (WTP) for cultural ES (Pascual et al., 2010). The recreational value of hunting was estimated through a revealed preference valuation method (Tietenberg and Lewis, 2016), using the price of licenses for the hunted species. The recreational value of forests was estimated based on the results of a previous study, which assessed the economic value for recreation in Swiss forests (Von Grünigen et al., 2014). Additional details about ES valuation are available in Appendix B.

The precision and resolution of ES supply maps depend on the availability of data for ES indicators. To visualize the distribution of the TEV from ES in the study area, individual ES maps (based on the map of ecosystem types) were overlaid as a single raster layer in ArcGIS 10.2. A summary of indicators, units and valuation methods used to quantify, map and value each service is available in Table 1.

2.4. Biodiversity mapping

Species distribution model (SDM; Guisan et al., 2017) maps were imputed as features in Zonation to identify priority areas for plants (n = 627 species), amphibians (n = 5), reptiles (n = 12) and insects (including orthopterans, bumblebees and butterflies, n = 123; see Vincent et al. (2019) for a complete list of species and modelling details). Observational data (random stratified sampling and opportunistic observation) in the study area of the *Vaud Alps* were related to a set of topo-climatic variables at a 25 m resolution (as used in previous studies; Dubuis et al., 2011; D'Amen et al., 2015; Pittet, 2017; Scherrer et al., 2017, 2019; Vincent et al., 2019) to model the current distribution of species using an 'ensemble of small models' approach (ESM; Breiner et al., 2015) based on three modelling techniques: Generalized Linear Models (GLM; McCullagh, 2018), Random Forests (RF; Breiman, 2001) and Maximum Entropy (MaxEnt; Phillips et al., 2006; Phillips and Dudík, 2008). A weighted mean of the three techniques was computed for each small model, with the predictive performance of each model estimated through split-sample cross-validation (75% for calibration, 25% for validation) and the maximisation of the True Skill Statistic (maxTSS; Liu et al., 2005) was used as a weight in the final ESM, also evaluated by maxTSS. For each species, the probability-threshold of the maxTSS was used to transform the probability predictions into binary presence-absence predictions. A land-use filter was also ultimately applied (setting predictions to zero) to remove any predicted presence that occurred in any land-use type without observation for the species. The final biodiversity component to be used in the Zonation analyses resulted from the stacking of all species' binary predictions across the study area (i.e. richness by stacking species predictions; α-diversity; see Dubuis et al., 2011) weighted by the species' conservation status (see Section 2.5).

2.5. Spatial conservation prioritisations with the Zonation software

To identify priority areas for biodiversity and ES in the *Vaud Alps,* the software Zonation 4.0 (Lehtomäki and Moilanen, 2013) was used. It produces a hierarchical prioritization of the landscape based on input factors and an iterative pixel removal rule that allows the retention of only the pixels contributing the most to specific conservation goals (Moilanen et al., 2014). Biodiversity information was integrated into the analysis by using the stacked SDM maps that are increasingly used in conservation planning (Guisan et al., 2013). Input factors from a previous prioritization analysis of biodiversity in the same study area (Vincent et al., 2019) were added, with the additional integration of the ES value maps created here. Inputs used here were: i) the maps representing ES economic values, and their values normalized from 1 to 100 as described by Casalegno et al. (2014); ii) the distribution maps with one map for each species, weighted by its priority status (see below); iii) land use maps (from Swiss land use statistics data from 2009; SFSO, 2013); and iv) political costs estimated from the opposition results from political votes that have a direct impact on biodiversity conservation (Cardoso, 2015; Vincent et al., 2019). The Additive Benefit Function removal rule was applied (Moilanen et al., 2014).

Each feature added to the Zonation analyses was assigned a weight, and the aggregated weight of features in each pixel defined its priority during the pixel removal process, with higher weights being given a higher priority (Moilanen et al., 2014). Species feature weights were first assigned based on species national IUCN Red List status with critically-endangered (CR) species given a weight of five, endangered (EN) species four, vulnerable (VU) species three, near threatened (NT) species two, and least concerned (LC) or deficient data (DD) species a value of one. Here, all statuses were assessed at a national scale (Moser et al., 2002; Schmidt and Zumbach, 2005; Monney and Meyer, 2005; Wermeille et al., 2014; Monnerat et al., 2007), except for *Bombus* spp. because the national assessment of hymenopterans was not yet available. In the latter case, the IUCN European Red List of Threatened Species was used (Collen et al., 2016). Second, an additional two weight points were assigned to any species that are protected under Swiss legislation. The Swiss protection status of each species was outlined by Cardoso (2015) and included species that are explicitly referenced in legislative documents. This resulted in weights assigned between one and seven for all species. Differential weighting between taxa was not used as we were interested in protecting overall diversity. See also Vincent (2017) and Vincent et al. (2019) for more details on these weight assignments. The sum of weights for all species in the analysis was equal to 961.

To account for prioritization based on the other land use types in the study area, negative weights were given to less favourable land use types. Of the seven land use categories, three were given negative weights: Intensive Agriculture −100, Pasture Agriculture −50, and Other (which includes glaciers, and alpine sports facilities, among others) −25. Closed forest, Open Forest, and Overgrown areas were not assigned a weight.

Since weights allocated to biodiversity features are determinant for the output of spatial prioritization, ten different weighting scenarios were tested for ES. Weight values ranging from 1 to 10,000 were

Table 2
Zonation solutions for different ES weights. Average proportion the study area remaining in the new conservation networks for α-diversity (species) and ES. Number of biological features (species and services) that have none of their range included in the proposed Zonation conservation network. Spatial overlap of different Zonation scenarios with existing protected areas (i.e. IUCN categories Ia and IV representing 18.12% of the study area) and the α-diversity network obtained without ES in the Zonation analysis.

Zonation solutions	Average proportion remaining in % for		Features not included in the network	Spatial overlap in % with		% of weight for services in the analysis
	α div	Services		Existing reserves	Zonation solution without services	
Existing reserves	25	10	1	100	34	0
α diversity only	44	17	0	34	100	0
Services weight						
1	43	19	0	33	82	1
10	42	25	0	33	76	9
25	40.3	31	0	30	70	20
50	38	35	0	28	66	34
75	36	39	0	26	61	43
100	35	41	0	23	52	50
200	30.8	45	0	19	44	67
500	25	48	0	13	32	83
1000	21.7	49	0	11	28	91
10′000	18.7	50	2	9	23	99

assigned to each of the ten ES selected. Since the sum of weights for species was already fixed to 961, a weight of 1 per ES, implying a total weight of 10 for all ES, means that they represent ca. 1% of the total weight in the analysis and biodiversity represent 99% of the total weight. Conversely, a weight of 10,000 per ES, implied that all ES represent 99% of the total weight in the analysis. Ten different scenarios were tested, with Biodiversity-only, ES-only (i.e 99% of weight) and 8 different weightings for ES (1%, 9%, 20%, 34%, 43%, 50%, 67%, 83%, 91%, 99%; Table 2).

The different Zonation solutions obtained for the ten scenarios were compared to see if the integration of ES changed the locations of prioritized areas and the efficiency of conservation networks for biodiversity protection, and how the weights given to them influenced the outcome. For each scenario that includes ES with biodiversity, the spatial overlap with existing protected areas (i.e. IUCN protected area categories Ia and IV), and with the Zonation solution focusing on biodiversity only, was calculated. The top 18.12% of the landscape, corresponding to the coverage by existing protected areas, was identified for each Zonation output map. The average proportion of protected species ranges and the number of species that have none of their range protected by the new protected areas were calculated for each scenario, to assess the efficiency of each proposed conservation network.

3. Results

3.1. Spatial patterns of ES, biodiversity and their covariations

The spatial distribution of the TEV for ES, through overlaying all individual services, is shown in Fig. 4A, B, D with related statistics. Maps of individual ES used as input for Zonation analyses are available in Appendix C (Figs. S1-S3). The TEV is geographically not evenly spread within the study area (Fig. 4F). Higher values are more present in the west of the study area, compared to lower values in the north-east. The absence of a value in the grey areas of the map, mostly occupied by urban areas, croplands, and areas with low-stature vegetation, is due to the selection of ES included in this study, as some ecosystems could not be assigned any ES value. Low economic values (< 500 CHF/ha/year) are distributed between 320 and 2000 m elevation. TEV of zero are present at low altitude, with higher values increasing to altitudes of 1500–1700 m (Fig. 3C). We observed a high TEV density in the altitudinal range 1000–2000 m, with values ranging from 1,500–20,000 CHF/ha/year (Fig. 3C).

The spatial distribution of biodiversity, through overlaying all individual species, weighted by their conservation status, is shown in Fig. 4C with related statistics. Mapped values thus represent weighted richness scores. Areas of low biodiversity predictions (coldspots) are primarily found in the western part of the study area (Fig. 4E), characterized by low altitudes (< 500 m) and by urban and cropland land cover types, and secondarily in the north-east (major area cover by grassland with few plant species). Biodiversity hotspots (scores up to 220) are located next to the coldspots in the western lowlands, where the relief starts to steepen and where forests become more developed, as well as toward higher elevations in the south-east. Weighted richness scores range from 0-165 across the sampled elevation gradient (320–2400 m), with two clusters of higher densities within the elevation range 1500–1700 m, one cluster with scores around 20, and another at ca. 75–100 (Fig. 3A). All of the pixels comprising scores greater than 200 are located between 1000–2000 m.

The majority of non-zero values for biodiversity and ES (as measured by TEV) across the study area are in the range of 5–150 for the weighted richness score and 200–30,000 CHF/ha/year for ES respectively (Fig. 3B). Two clusters stand out due to the inverse relationship between ES and biodiversity. The first for a TEV around 500 CHF/ha per year for biodiversity scores around 75–100, and a second in the range of 3000–5000 CHF/ha per year with biodiversity scores lower than 50 (Fig. 3B). Pixels with biodiversity scores greater than 175 are associated with a TEV of up to 35,000 CHF/ha/year. The biodiversity score decreases linearly to values lower than 75 for the highest TEV (ca. 950,000 CHF/ha/year).

It is useful to look at the distribution of biodiversity and TEV within land cover (Fig. 4B) because land cover (incl. land use) is an important layer in the mapping of ES and in the building of SDMs. The TEV values throughout the study area are linked to land cover types located between 1000 and 2000 m (i.e. grassland, coniferous forest, mixed forest, heathland and shrubs, woodland and forest). Only the lowest TEV values (< 500 CHF/ha/year) are linked to land cover at low altitudes (urban, cropland, wetland, rivers and lakes) with the exception of sparse vegetation land cover (low TEV and high altitude) (Fig. 4A-D). Fig. 3A and Fig. 4A-C show that the pixels with diversities between 0 and 125 species at low altitudes are found in cropland and urban areas (15% of the territory), but also in wetlands and rivers and lakes. The areas of low diversity at 1500 m (Fig. 3A) is explained by the woodland and forest land cover which tend to have lower diversity for the species included in this study (Fig. 4C). Another hotspot at the same altitude but with a higher biodiversity score (75–100) is mainly associated with heathland and shrubs, coniferous forest and grasslands representing

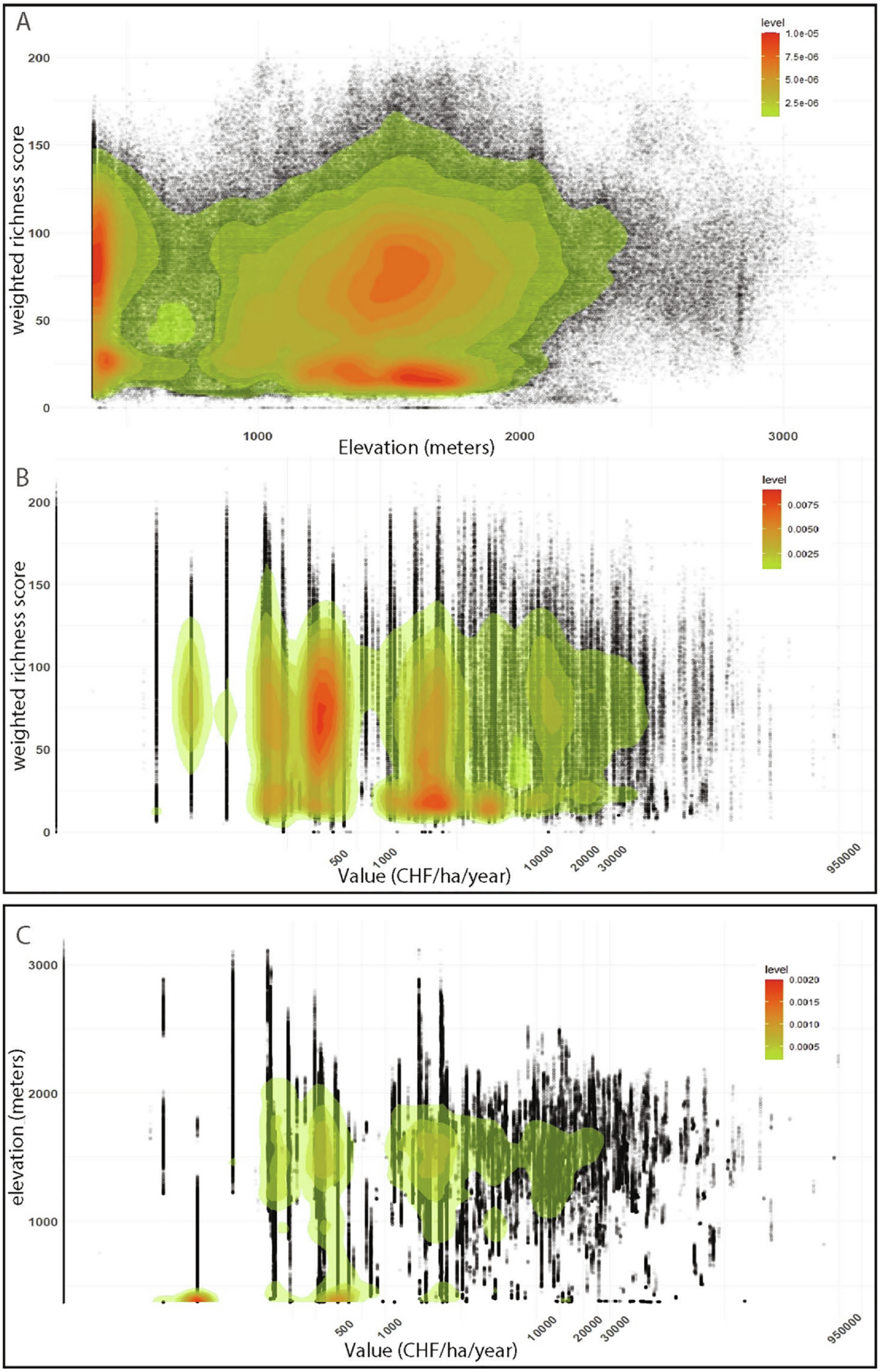

Fig. 3. Heat plot of the weighted richness score in function of the elevation (m) and the TEV (CHF/ha/year) (A-B, respectively). Heat plot of the TEV in function of the elevation (m) (C). Green indicates a lower density and the orange a higher density of points.

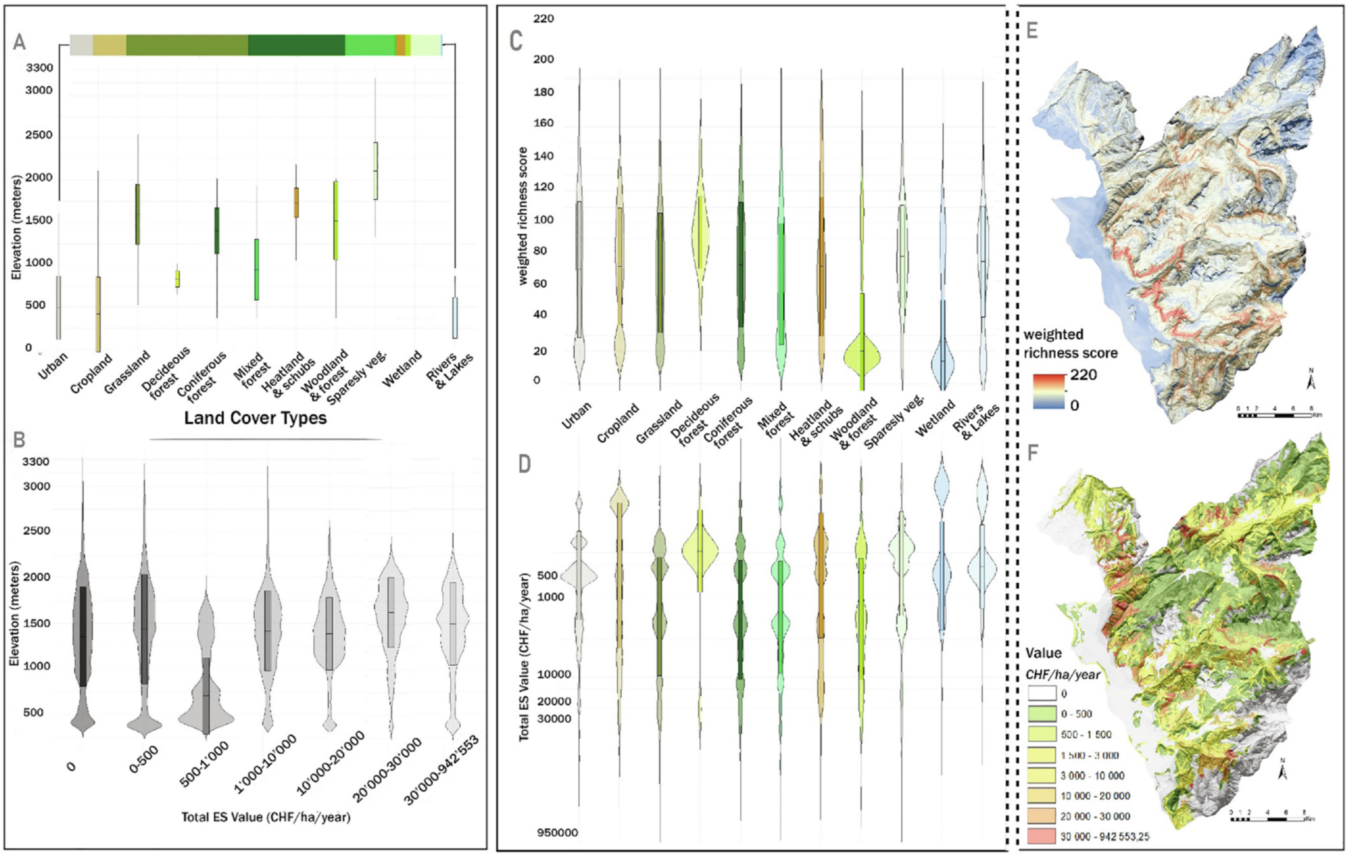

Fig. 4. Analysis of the distribution of the TEV per site (CHF/ha/year) and the diversity (N species) in function of the elevation and the land cover types (LC). We show the distribution of LC (A) and the TEV of ES (B) in function of elevation with a violin plot. Diagram indicates the proportion of each LC on the study area. The last violin plot (C-D) show respectively the distribution of the weighted richness score and the TEV of ES into the different types of LC. The box inside each violin represents +/- the standard deviation and the crossbar is the median. (E) Biodiversity predictions resulting from stacking binary (presence-absence) predictions of all species weight (n = 961) in the study area. Coldest colors (blue) indicate a low score (e.g. West side in the urban area), hottest colors (red) indicate a high score (e.g. forest slope on the middle of the study area) (see Vincent et al., 2019). (F) Distribution of the TEV calculated for a subset of ES within the study area of the Vaud Alps. The grey areas correspond to arable land outside irrigation perimeters and urban fabrics, disjoint and sparse agricultural areas, or rocks and glaciers. Any ES value in these grey areas (not yet quantified).

60% of the study area. The deciduous forests cover a very small zone of the study area despite having a fairly high median biodiversity score (ca. 100). The slope is not the element explaining the distribution of the biodiversity score. Intersecting maps of biodiversity (Fig. 4E), ES (Fig. 4F) and land cover (Fig. 2) reveal these patterns.

3.2. Zonation prioritization solutions

When ES are included in the analysis, priority areas for conservation differ from those selected by prioritising biodiversity only (Figs. 5 and 6; Table 2). The spatial overlap between the location of existing protected areas (Fig. 5A) and biodiversity (Fig. 5B) is 34%. With the increase in weight for ES, the spatial overlap between Zonation solutions and existing protected areas decreases (Table 2). These changes in areas to prioritize are represented in Fig. 5C–H. The priority areas selected by Zonation focusing only on ES are predominantly located on the north-western side of the study area (Figs. 5H and 6D). Conversely, areas selected by Zonation focusing only on biodiversity (Figs. 5B and 6D) are more represented in the south-eastern part of the study area. As the weight for services increases in the analysis, the prioritization zones become increasingly similar to the prioritization solution based on ES only (Fig. 5H). This trend is visible in Fig. 6, representing the spatial overlap between ES only, biodiversity only and the weighting scenarios (Table 2).

A low weight for ES in the analysis (9%) implies a high spatial overlap (> 75%) with prioritizing biodiversity only (Fig. 5A). In this case, the performance of both conservation networks is comparable since the biodiversity prioritization covers on average 44% of all species ranges and the biodiversity and ES prioritization covers 42%. For the same scenarios, the average ES coverage in the new conservation network is 17% for biodiversity only and 25% for the biodiversity and ES prioritization, indicating that even a low weight for ES in the analysis induces an increase in ES protection.

The protected coverage of species ranges decreases when the ES weight increases in the analysis. However, the coverage remains higher than the average species range protected by existing protected areas (25%) for Zonation solutions when ES represent up to 83% of the weight of the analysis. When the weight for services surpasses 83%, the Spatial Conservation Prioritization scenarios result in solutions with lower protection of biodiversity than existing protected areas (i.e. the average protected species range is lower than 25%). The extreme scenario with services representing 99% of the weight in the analysis (i.e. each service has a weight of 10,000) results in an average protected species range of only 18.7% (Appendix C, Fig. S5-6).

3.3. Relationship between spatial conservation planning analyses and input ES and biodiversity maps

Existing protected areas would not be optimally located to jointly protect biodiversity (weighted α-diversity here) and guarantee the ES supply (50/50 weights in the Spatial Conservation Planning analyses) in the Vaud Alps. However, those ES present in protected areas tend to

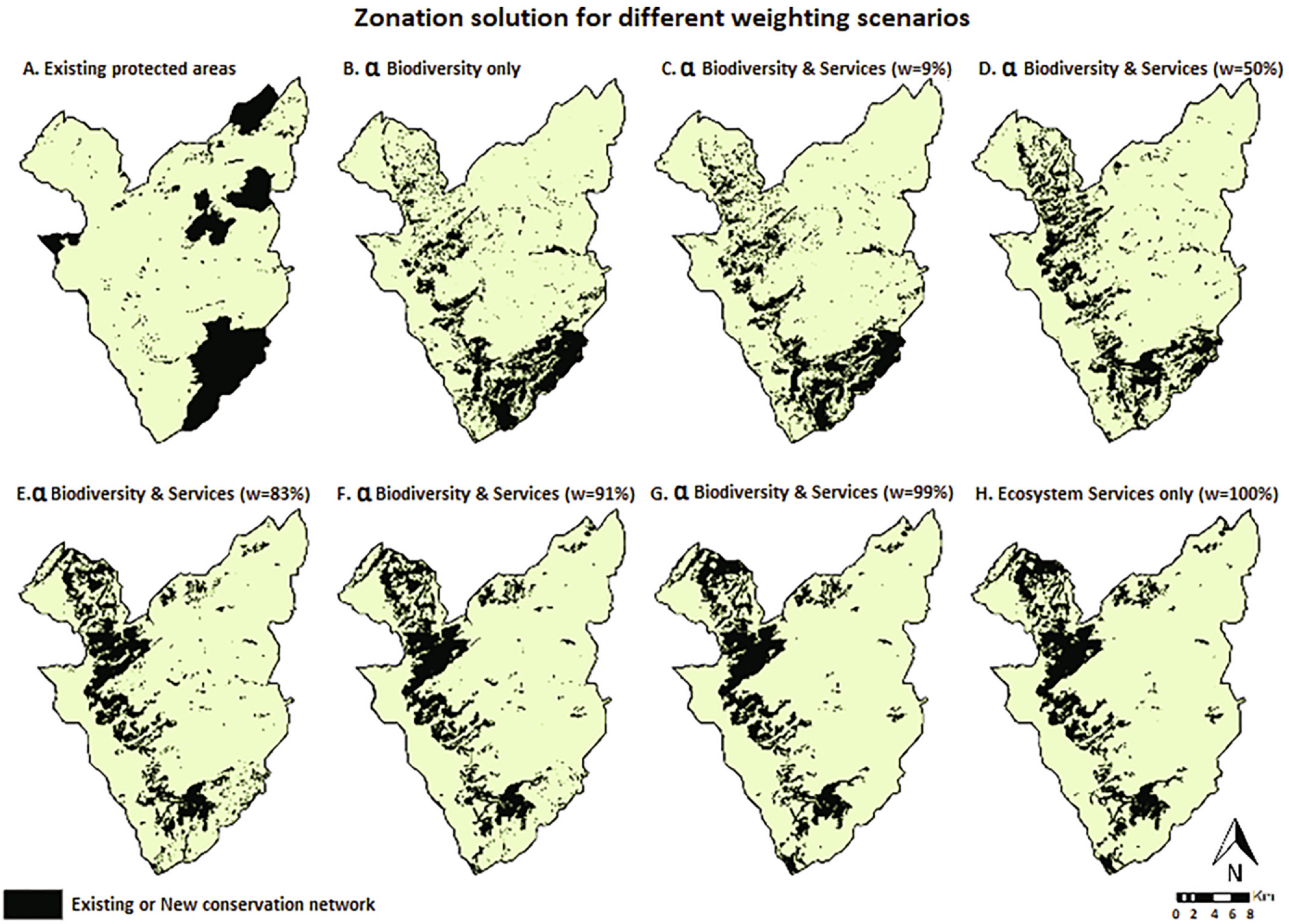

Fig. 5. Proposed protected areas under different scenarios. Existing protected areas (A), Zonation solution prioritizing biodiversity only (B), Zonation solutions for scenarios including biodiversity and ES with different weights(C-G) and Zonation solution focusing on ES only (H). The importance allocated to services compared to biodiversity in each scenario is given by the percentage of weight for services (w). The top 18.12% of priority areas selected by Zonation was extracted for each scenario, in order to keep the same proportion of the landscape in new conservation networks than existing protected areas.

have high TEV (> 3000 CHF/ha/year; Figs. 3, 4 and 6A) compared with the average economic values of the different land cover types. When focussing only on the distribution of biodiversity, only protected areas of IUCN category Ia (southern part of the study area) are important for biodiversity (Fig. 6). The optimal areas for biodiversity and ES tend to be located in peri-urban wooded areas in the montane zone (1200–1800 m), where a trade-off exists between biodiversity and the areas with ES between 1,500 and 30,000 CHF/ha/year (Figs. 2–4).

Although the highest values of biodiversity and ES are expressed at the same altitudinal range, they are not geographically overlapping (Figs. 3 and 4). If we look at the individual taxa richness maps (Appendix C, Fig. S4A-D), areas of low general biodiversity importance for plants and insects (e.g. cropland, wetland, rivers and lakes) can be priority areas for reptiles and/or amphibians. The observation is the same when focusing on threatened and protected species only, hotspots for which are found at areas with average biodiversity values (central-east of the study area; Appendix C, Fig. S4E). Only hotspots for reptiles overlay with hotspots of TEV for ES (Fig. 6, Fig. S4D).

4. Discussion

This study is among the first to combine elements of biodiversity and ES in the same spatial conservation planning framework (as e.g. Chan et al., 2011; Cimon-Morin et al., 2013; Xu et al., 2017; Reale et al., 2019; Honeck et al., 2020) for a whole mountain region. To date, assessments in the Alps and other mountain regions integrated only one of these two components at a time (Grêt-Regamey et al., 2008a, 2008b; Lavorel et al., 2011; Falcucci et al., 2013; Vincent et al., 2019). Furthermore, still very few considered species distribution models (as in Vincent et al., 2019) to provide a spatial component to the distribution of biodiversity as an input for Spatial Conservation Planning (Tulloch et al., 2016), and even more in mountain regions that are sparking growing interest in ES and biodiversity (Lavorel et al., 2020). The primary objective of Spatial Conservation Planning is to find the best compromise between the use of a territory as driven by socio-economic activities and the maximization of biodiversity protection within a territory (Bruni, 2018). Using a Spatial Conservation Planning framework combining mapped data for biodiversity (Vincent et al., 2019) and ES (Grêt-Regamey et al., 2012; Diaz et al., 2015), we investigated here whether accounting for these two components equally could lead to distinct prioritization solutions (as e.g. in Chan et al., 2006). We illustrated the approach with the species richness (α-diversity) of plants, amphibians, and reptiles and three subgroups of insects as the biodiversity components and a selection of ten ES representing quantifiable provisioning, regulating, and cultural services in a study area of the Western Swiss Alps. Our key results are that: (i) giving too much weight to ES can increase the related economic benefits but at the expense of biodiversity protection. This corroborates the finding of Chan et al. (2006) that a strategy which combines ES and biodiversity cannot fully substitute for targeted biodiversity protection; and (ii) protected areas are currently not optimally located to ensure prioritization of both ES and biodiversity. As future improvements, we recommend conducting

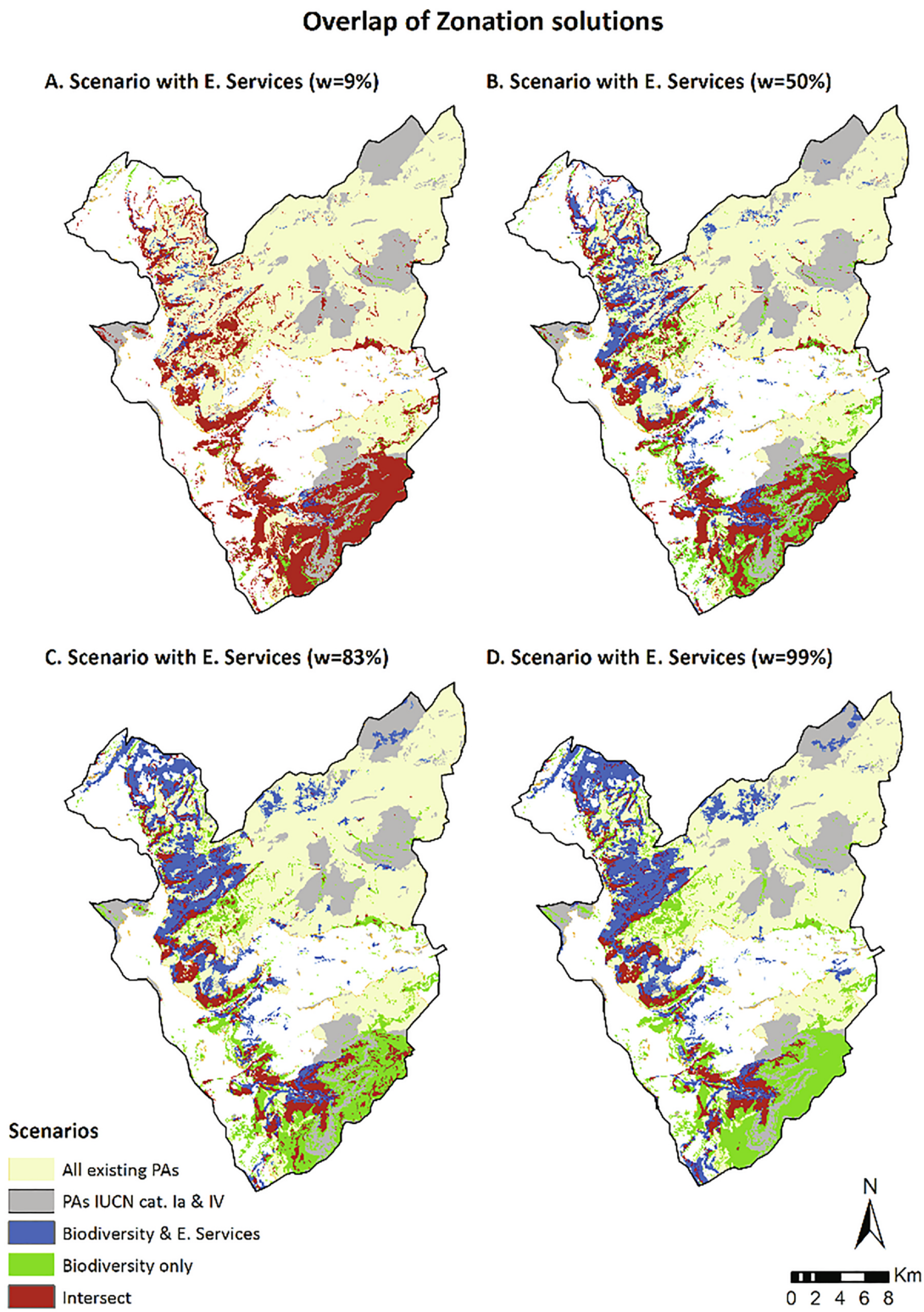

Fig. 6. Comparison between Zonation solutions created by overlaying the solution obtained with α-diversity only with solutions additionally including ES, with the latter representing: 9% (A), 50% (B), 83% (C) and 99% (D) of total weights in Spatial Conservation Planning analysis. The overlapping regions (i.e. prioritized in both solutions but with different weights) are shown in red. Areas prioritized by analysis including α-diversity and ES are shown in blue. Areas prioritized by analysis focusing only on α-diversity are shown in green. Existing protected areas (protected areas; IUCN categories Ia and IV) are shaded in grey and the other protected areas with lower levels of protection are represented in yellow.

Spatial Conservation Planning with a more comprehensive coverage of biodiversity (e.g. soil biota, genetic and ecosystem diversity) and ES (e.g. non-monetary) components.

4.1. Differential priorities for ES and biodiversity with relation to existing protected areas

This study highlights the importance of prioritizing entities of biological value (here α-diversity and ES) through the weights assigned to them in Spatial Conservation Planning analyses (as in Vincent et al., 2019 for biodiversity), and more generally in any decision-making process (Arponen et al., 2005; Di Fonzo et al., 2017). Increasing the relative importance of ES in the analysis led to a decrease in the protection of biodiversity. This result highlights the trade-off often observed between ES and biodiversity (Naidoo et al., 2008; Mace et al., 2012), and more generally between the different characteristics to be prioritized (Kovács et al., 2015). Our results thus illustrate the potential consequences of setting alternative priorities, like favouring ES, for the protection of biodiversity (Kukkala and Moilanen, 2017). Different weighting scenarios for ES can be seen as simulating different political decisions (e.g. conservation or economic objectives) and the different ranges of species protected by new conservation networks represent the consequences of simulated actions for biodiversity (Guisan et al., 2013).

This type of analysis shows that including ES in conservation planning, even with little weight in the analysis (9%, Table 2), can stabilize the protection of certain ecosystems rich in taxa (less than 2% decrease in biodiversity within protected areas) despite an increase in ES (+15% of the coverage of the study area and +8% within protected areas), as also reported elsewhere (Snäll et al., 2016). This ES-enriched framework could be used by policy makers to not only value profitable ES, which as we showed could decrease biodiversity protection, but also non-profitable ones that could better ensure biodiversity preservation (Tratalos et al., 2016). Sustainable management of ecosystems in protected areas could be expected to further help achieve this objective (Smith et al., 2016). Such a decision-making tool, combining ES and biodiversity, could be particularly useful for promoting sustainable economic development that does not jeopardize the Alpine biodiversity that is very sensitive to changes in ES supply (Grêt-Regamey et al., 2008b; Gupta et al., 2019).

Decision-makers would typically have the task of assigning values for these weights, balancing the importance of ES with that of biodiversity based on the available information and future challenges (Martínez et al., 2009). Additionally, compromises would need to be made between different ES provided by the same ecosystem (Turkelboom et al., 2016). For example, wood supply, carbon sequestration and hydrogeological protection services are provided by forests, but timber harvesting involves the loss of carbon sequestration and protection services (Pang, 2017). Hence, the silviculture and forest management systems may have an impact on the climate regulating effects (Naudts et al., 2016). Risks related to high winds are also not considered here, but may vary between coniferous and deciduous forest ecosystems (Matthies and Valsta, 2016). Choosing one service over the other will then potentially have cascading effects on aspects of biodiversity conservation (Kandziora et al., 2013). This type of trade-off is particularly visible in the Vaud Alps, where many forests are considered as protective against natural risks (Federal law on the forest (921.0) (Anon, 2017); Moos et al., in review), and are therefore not exploited intensively for the production of wood, but rather managed to maximize their protective role (Grêt-Regamey et al., 2008b). The question whether biodiversity and ES should be treated separately or together in Spatial Conservation Planning analyses is still debated (Chan et al., 2006, 2011; Cimon-Morin et al., 2013). In the case of identified trade-offs between biodiversity and ES, the decision will depend on the preference of stakeholders for specific conservation objectives (Kukkala and Moilanen, 2017).

4.2. Comparing spatial patterns of ES, biodiversity and protected areas within the study area

The variations of ES and α-diversity within the study area revealed complex patterns, with some rather limited co-variation. The elevation zone 1200–1800 m tended to include both the highest densities and values for the biodiversity components assessed here and for the TEV of ES (Figs. 3 and 4), which supports the hypothesis that a peak in α-diversity can correspond to a peak in ES (Costanza et al., 2007), especially in studies assessing recreational ES with biodiversity (Assandri et al., 2018; Mancini et al., 2019; Tuan et al., 2019). However, the coinciding of biodiversity and ES peaks at the same elevation zone does not mean they spatially overlap, and can be interpreted in our area by both the presence of ski resorts (Leysin (low alt = 1328 m; high alt = 2200 m), Villars-Gryon (low alt = 1100 m; high alt = 2000 m), Les Diablerets (low alt = 1380 m; high alt = 2970 m)) and the mix of forests and grasslands at these elevations, increasing both the ES benefits (Schuler et al., 2017) and the α-diversity respectively.

A result that could seem surprising is the lack of priority areas for ES and biodiversity in lowland areas, but this is likely explained by the presence of urban landscapes in these areas causing lower biodiversity (Habel et al., 2019; Salaverri et al., 2019) and because this study did not consider specialized ES for urban land cover types. In other places, the biodiversity scores were lower where the ES values were high (e.g. the north and the north-west of the study area - "*Parc Gruyère Pays-d'Enhaut* - Fig. 4E, 4F and 6), but the reverse was rarely observed. While comparing the different figures in Appendix C (Figs S1-S4), we can observe that such low overlap (between biodiversity and ES) is mainly true for the provisioning services, at the exception of the milk provision. Concerning the regulating services, the area with the highest values are too small (in terms of area) to be compared with the hotspot of species diversity. And finally, for the cultural services, only recreation forests can present a conflict regarding the interaction with biodiversity (creation of lines/axes of perturbations). To conclude, overall there was a trade-off between biodiversity and ES, across all types of ES.

Finally, protected areas tend to be more efficient at preserving biodiversity than supporting ES, whereas ES tend to have greater values in anthropized areas (Fig. 2, 4E-F). When focussing only on the distribution of biodiversity, only protected areas of IUCN category Ia (southern part of the study area) appear important here (Fig. 6). Although wetlands are poorly represented in our study area, considering both wetlands and peatlands in protected areas could add an ES value for carbon sequestration (Hansson et al., 2005). More importantly, our results suggest that protected areas of IUCN category IV (e.g. Natura 2000) are not systematically the best areas to protect biodiversity and ES (Maes et al., 2012; Cardoso et al., 2015).

4.3. Limitations & perspectives

At each stage of the proposed Spatial Conservation Planning framework (Fig. 1), choices were made regarding the methods and parameters. We discuss below some limitations and uncertainties associated with these choices, which can influence the spatial prioritization results, and propose some potential ways forward.

The subset of ES included in this study tended to value forests disproportionately, since eight of the ten selected/available ES were related to forest ecosystems, while biodiversity represented open habitats disproportionately. The reason for this was that data concerning open (non-forest) habitats and other landscapes were not available to estimate ES at the start of this study (Appendix A - Table A3). It is therefore important to consider running more comprehensive analyses in the future, with: (i) more taxonomic groups in all ecosystem types, such as birds, mammals, other invertebrates (such as saproxylic beetles), and soil biota and different ways to rank conservation value because IUCN Red Lists are not optimal (Collen et al., 2016); here, only plants, reptiles and amphibians covered also forests; (ii) biodiversity facets other than α-diversity, such as β-diversity (e.g. Pellissier et al., 2013), genetic and ecosystem diversity or functional dimensions (e.g. D'Amen et al. 2018), to account for the species ability to cope with climate and other environmental changes; (iii) more ES; only 10 were used here, with forest ES being slightly over-represented (6/10), likely due to a historic bias toward forestry research in Switzerland (Loran et al, 2017); other ES could include (see suppl. table A3): the aesthetic value of the landscape (Grêt-Regamey et al., 2007; Lavorel et al., 2020), scenic value (Schirpke et al., 2013), outdoor activities (e.g. through GPS tracking, Byczek et al., 2018), water provision for the lowland populations (Leitinger et al., 2015), or the potential for recreational activity (Lavorel et al., 2020), and cover the whole range of habitats, from open to forested. The selection of biodiversity and ES components for such a study should be meaningful for the study area and originate from an agreement between scientists and stakeholders on the Spatial Conservation Planning objectives (Guisan et al., 2013; Moilanen et al., 2014), and be standardized at the relevant scale (Jaligot et al., 2019); and (iv) better data; bias (e.g. in geographic and environmental coverage; Bird et al., 2014) can affect both the data - especially citizen science data (Clare et al., 2019) as used here for amphibians and reptiles - and the models based on these (Guisan et al,., 2013; Tulloch et al., 2016). Methodologies to improve model predictions (Phillips et al., 2009; Fithian et al., 2015; Burkhard and Maes, 2017) represent useful perspectives to improve Spatial Conservation Planning.

To complete the valuation of ES, as for non-forest habitats in this study, two additional types of values could be considered: ecological and socio-cultural (Brondizio et al., 2010). Ecological value is represented by the integrity, health or resilience of ecosystems (Müller and Burkhard, 2010). The socio-cultural value comes from the intangible well-being provided by nature to people, implying ethical, religious or spiritual values (Diaz et al., 2015). These values cannot be fully estimated by economic valuation and require the development of alternative parameters (De Groot et al., 2010a, 2010b). In this regard, it would be important to find valuation methods that better represent cultural ES, such as outdoor activities and scenic beauty (Grêt-Regamey et al., 2007; Schirpke et al., 2013, 2016; Byczek et al., 2018), to give more weight to these areas, which can be rich in biodiversity but where the latter can in turn suffer high disturbances related to tourism (Tolvanen and Kangas, 2016). Sites near winter sports resorts may also require a stronger compromise between biodiversity and ES (Byczek et al., 2018; Lavorel et al., 2020). In this way, a comprehensive assessment of the value of nature, for the different types of ecosystems present in the study area, could be used to improve conservation planning.

The choice and availability of indicators used to quantify and evaluate ES can also be a source of uncertainty (Cimon-Morin et al., 2013; Vincent et al., 2019). The use of different indicators and assessment methods can for instance lead to different results for the same ES (Burkhard and Maes, 2017). One reason for this is the lack of well-defined methodologies for estimating the non-instrumental (i.e. intrinsic) value of nature (Gómez-Baggethun et al., 2014; Small et al., 2017). This also explains the bias in the literature in favour of marketed services (Brander and Crossman, 2017). In addition, any ES evaluation method will strongly depend on the social, cultural and economic contexts of the study, for example hunting (Schmidt, 2000; Bang and Dahlström, 2009); hydrogeological protection services (Barth and Döll, 2016; Brander and Crossman, 2017); or the costs of replacing forests with a technological substitute (Notaro and Paletto, 2012; Brander and Crossman, 2017). For this, it would be interesting to work with several methodologies (and different software; Burkhard and Maes, 2017) and assess how these affect the Spatial Conservation Planning outcomes.

Finally, future studies should integrate all important biodiversity and ES components into more comprehensive conservation plans (Kandziora et al., 2013), additionally including the service suppliers (ecosystems/habitats), and all key external drivers (climate change, invasive species, habitat change, exploitation, pollution, or change in nutrient content; Vicente et al., 2011; Maes et al., 2012; Harrison et al., 2014; Lee and Lautenbach, 2016; Burkhard and Maes, 2017). In particular, whereas climate change is often assessed (e.g. Vincent et al., 2019), also accounting for effects of land use changes (Gago-Silva et al., 2017), the spread and impact of invasive species (Vicente et al., 2011; Petitpierre et al., 2016), and other pressures (Thom and Seidl, 2016) will remain a major challenge for building sustainable action plans for biodiversity and ES in mountain ecosystems (Schirpke et al., 2017).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2020.101186.

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