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Climate and land-use changes reshuffle politically-weighted priority areas of mountain biodiversity

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ABSTRACT

Protected areas (PAs) play a critical role in conserving biodiversity and maintaining viable populations of threatened species. Yet, as global change could reduce the future effectiveness of existing PAs in covering high species richness, updating the boundaries of existing PAs or creating new ones might become necessary to uphold conservation goals. Modelling tools are increasingly used by policymakers to support the spatial prioritization of biodiversity conservation, enabling the inclusion of scenarios of environmental changes to achieve specific targets. Here, using the Western Swiss Alps as a case study, we show how integrating species richness derived from species distribution model predictions for four taxonomic groups under present and future climate and land-use conditions into two conservation prioritization schemes can help optimize extant and future PAs. The first scheme, the “Priority Scores Method” identified priority areas for the expansion of the existing PA network. The second scheme, using the zonation software, allowed identifying priority conservation areas while incorporating global change scenarios and political costs. We found that existing mountain PAs are currently not situated in the most environmentally nor politically suitable locations when maximizing alpha diversity for the studied taxonomic groups and that current PAs could become even less optimum under the future climate and land-use change scenarios. This analysis has focused on general areas of high species richness or species of conservation concern and did not account for special habitats or functional groups that could have been used to create the existing network. We

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conclude that such an integrated framework could support more effective conservation planning and could be similarly applied to other landscapes or other biodiversity conservation indices.

1. Introduction

Growing anthropogenic activities are causing increasing threats to biodiversity even in pristine areas (Lambin et al., 2001). Land-use change, human induced climate change, or the introduction of invasive species (Millennium Ecosystem Assessment, 2005) are affecting natural ecosystems, reducing the habitat available for species and therefore causing species extinctions and biodiversity loss (Steffen et al., 2007). The effects of climate change have already influenced species ranges, shifting them northwards and to higher altitudes (Walther et al., 2002; Hickling et al., 2006; Chen et al., 2011), causing some species to move out of current protected areas (PAs; Araújo et al., 2004). The fast rate of climate change might limit the capacity of species to adapt locally or to migrate to suitable areas (Welch, 2005). Land-use change can have further substantial and severe negative effects on biodiversity (Struebig et al., 2015), stressing some vulnerable species and pushing them closer to extinction (Gibson et al., 2011). These changes can lead to an overall decrease in species diversity in previously species-rich areas.

The international conservation community has identified PAs as the cornerstone of biodiversity conservation (CBD, 2010), protecting vulnerable species and habitats, with mountains playing a special role as species sanctuaries (Bugmann et al., 2007; Guisan et al., 2019). Due to legal constraints, terrestrial PAs are usually designed to be static, not accounting for ecosystem changes or shifts in species ranges, potentially limiting their effectiveness under climate or land-use change (Pressey et al., 2007; Alagador et al., 2014).

Systematic conservation planning is a spatial process designed to optimize the delimitation of PAs, by identifying a limited set of unique and/or complementary areas that maximize biodiversity conservation (Pressey et al., 2007). Financial resources are limited, therefore considering land costs makes conservation planning more effective, as it balances the costs of conservation with the benefits to wildlife (Newburn et al., 2005). Thus, incorporating land-use change and land costs into conservation prioritization analyses has the power to provide an added priority ranking of PAs (Naidoo et al., 2006). However, a PA network should be designed in such a way that it can be adapted to changing conditions, since the effects of climate change are now inevitable and cause species distributions to be non-static within landscapes (Heller and Zavaleta, 2009).

To include future scenarios of species distributions, predictions based on species distribution models (SDMs; Guisan et al., 2017) can be incorporated into the analyses (Guisan et al., 2013). A recent study reported that conservation planners could still make better use of SDMs, supporting further development of such quantitative tools in conservation planning (Tulloch et al., 2016). Prioritization tools for conservation planning, such as the “Zonation” software (Moilanen et al., 2005), support the identification of important areas while considering a cost-benefit ratio. Zonation can incorporate SDM predictions with cost maps, future landscape changes, species interactions, and habitat connectivity to find the optimal PA network based on predefined conservation goals. It has been used for conservation planning on a variety of projects around the globe (e.g. Summers et al., 2012; Faleiro et al., 2013; Pouzols et al., 2014), but we know only three examples where it was used in mountain areas (Fleishman et al., 2014; Wan et al., 2016; Zhang et al., 2011), none of which were in Europe or incorporating political costs.

Here, we used an existing prioritization method and compared it to a new multi-drivers framework within the Zonation software to assess existing PAs and propose a new PA network. We illustrate the approach through a case study in the Western Swiss Alps. The goal of this analysis was to propose an improved framework to identify the most cost-effective PA network that will protect the highest level of species richness across several taxonomic groups, and to investigate whether the areas identified by these two prioritization methods provide the same hotspots for protection. The analysis included species data for insects, amphibians, reptiles, and plants combined with environmental and landscape data within SDMs, and human socio-economic data (e.g. political costs). We then investigated the effects of climate and land-use changes on optimal conservation solutions and determined potential drawbacks and improvements to these prioritization methods. Additionally, based on this study, we identified possible gaps and ways forward to improve conservation planning in mountain and other regions.

2. Methods

2.1. Study area

The Western Swiss Alps of the Vaud canton were used for this case study as they represent a priority area for research of the new Center for Mountain Studies (CIRM) at the University of Lausanne (see https://www.unil.ch/centre-montagne) and benefits already from a large geoportal documenting on all existing data (http://rechalp.unil.ch). Due to its high diversity of species and of key conservation habitats, it was declared a priority area for conservation by WWF, Birdlife International and Pro Natura in 2015 (http://www.leregional.ch/N67958/la-position-du-wwf-et-de-pro-natura-en-detail.html) and a general conservation plan is currently under consultation. The elevation ranges from 375 m to 3210 m with an annual mean temperature between 3.5 °C and 8 °C, and the annual sum of rainfall between 1400 mm and 2400 mm (Randin et al., 2006).

In the study area, PAs were assigned to one of four tiers based on their international commitments to protect biodiversity (Table A1; Appendix A). PAs designated with the International Union for Conservation of Nature (IUCN) Category Ia "Strict Nature Reserve" are assigned to Tier 1, and IUCN Category IV "Habitat/Species Management Areas" to Tier 2. Tier 3 PAs do not align with these IUCN categories, even though they may have stronger national regulations. Tier 4 includes PAs that are not designed for biodiversity conservation, but which may indirectly protect nature. In the study area, 18.12% of the landscape is protected by either Tier 1 (0.02%) or 2 (18.1%) areas (Fig. 1). Although some of the existing PAs were created to protect a specific habitat (e.g. fens, bogs and alluvial zones) or a taxonomic group (e.g. amphibians), the goal of our analysis was to assess the hypothetical protection of the highest number of species within the most cost-effective area of land (i.e. alpha diversity; the analysis optimizes a different goal than the existing set of PAs).

2.2. Data sources

We fitted species distribution models (SDMs; Guisan et al., 2017) and derived spatial predictions as inputs for the conservation planning analyses for multiple species in four different taxonomic groups: insects, amphibians, reptiles, and plants (Table 1). Different sampling strategies were used to sample the different taxonomic groups: random stratified sampling was used to sample plants and insects, while occurrence records for amphibians and reptiles came from opportunistic observations in a national database (for a detailed description see Appendix C). SDMs predictions were based on 25 m resolution topoclimatic variables including monthly maximum and minimum temperature and sum of precipitations, annual growing degree days, annual evapotranspiration, topographic position, aspect and slope (for a detailed description see Appendix C). These variables have been shown to be useful predictors in mountain environments (D'Amen et al., 2015; Dubuis et al., 2011; Scherrer et al., 2017, 2019). Predictions for the future were based on variables translating the A1B climate storyline (IPCC, 2001) for the years 2045–2074 (from here on referred to as 2060) and calculated using the climatic anomalies for all Swiss weather stations (Bosshard et al., 2011). This future climatic scenario predicts the global average temperature to rise by 1.8 °C by 2060 (for a detailed description see Appendix C) and was chosen because is comparable with the land-use scenario available for this study.

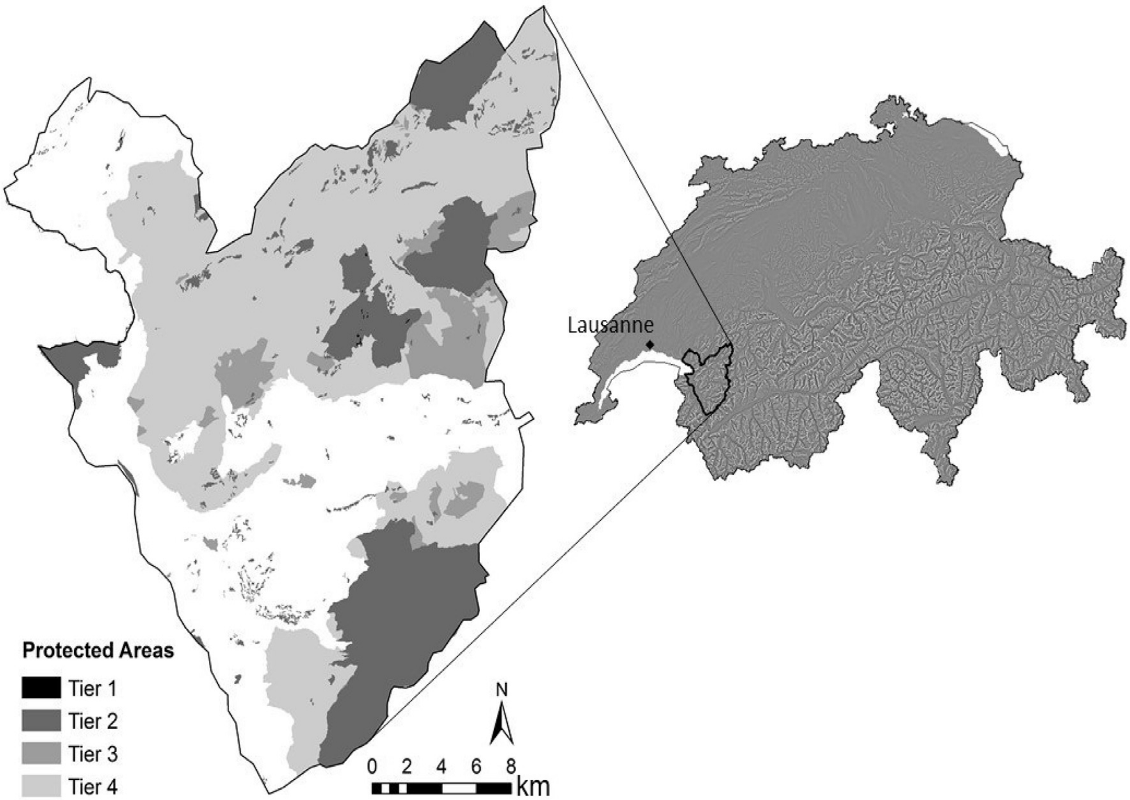

Fig. 1. The study site and its position in Switzerland. The current protected areas are shaded in grey with the highest level of protection (Tier 1) given the darkest color, and the lowest level of protection (Tier 4) shown with the lightest grey.

Table 1
A summary of the species list (see Appendix B for details), showing the number of species for each taxonomic group used in this analysis.

Taxonomic Group	No. of species	Threatened species (CR, EN, VU)[a]	Protected species[b]
Amphibians	5	2	5
Insects	123	3	4
Plants	627	4	47
Reptiles	12	9	12
Total	767	18	68

[a] Threatened species are based on the Swiss national Red Lists.
[b] Protected species are explicitly referenced in Swiss legislative documents.

The baseline land-use map was taken from the Swiss land-use statistics data from 2009 (SFSO, 2013; Fig A1a, Appendix A). The future land-use scenario map was modelled by Price et al. (2015) under the A1 climate change scenario (the scenario family in which A1B is found) using the Dynamic Conversion of Land Use and its Effects Model framework (Dyna-CLUE; Verburg and Overmars, 2009) for the year 2035 (Fig A1b; Appendix A). This model predicts high levels of agricultural land abandonment, especially in mountain pastures, and urbanization in lower elevation areas near roads and existing towns. Under this climate scenario there is more afforestation, defined as a transition from any land use to forest, than any other scenario.

2.3. Species distributions models

We used an ensemble of small models (ESMs; Breiner et al., 2015) to predict the current and future distributions of 767 species (Table 1) based on environmental data at high resolution (25 m). ESMs were implemented to avoid overfitting and to improve the modelling of rare species as they fit and average many small models each with few predictors at a time (typically 2) weighted by their cross-validated predictive performance (Lomba et al., 2010; Breiner et al., 2015). While ESMs were designed to model species with small sample sizes, they also work well for common species (Breiner et al., 2015). Only species with at least 10 presences were modelled (see Appendix B for the number of presences/absences for each species). A weighted mean of the following three modelling techniques was used to predict species distributions based on observational data and environmental variables: generalized linear models (GLM; McCullagh and Nelder, 1989), random forests (RF; Breiman, 2001) and maximum entropy (MaxEnt; Phillips et al., 2006; Phillips and Dudik, 2008).

The data for each species was randomly partitioned into 70% for calibration and 30% for validation and this procedure was repeated 5 times. For each combination of two environmental predictors, the different models were evaluated using a maximization of the True Skill Statistic (maxTSS; see Appendix B for values), taking both omission and commission errors into account (see Appendix C for details on ESM parameterization). Predictions were turned into binary presence-absence maps using the same thresholding approach that maximizes the TSS (Liu et al., 2005) for both current and future distributions. Another map was saved for each species after applying a land-use filter which removed any projected presence that occurred in a land-use type in which no observations were recorded. Additionally, the species binary maps were summed, across species of an interest group, to create different diversity maps.

2.4. Spatial prioritization methods

Two methods of spatial prioritization for biodiversity conservation were compared (Fig. 2). First, the “Priority Scores Method” (Fig. 2a; Jenkins et al., 2015) identifies priority areas for the expansion of the existing PA network. It enables planning to be focused on target species having the greatest need for protection. Second, the “Zonation Land-Use Filter Method” (Fig. 2b) uses the Zonation software to combine the effects of climate change, land-use change, and land costs to propose optimal conservation areas and to assess the current PAs' ability to protect species richness. The priority scores were calculated with both the current and future predicted species distributions. These methods both generated maps with continuous ranking of the landscape to identify conservation priorities.

The priority scores method is based on the proportion of the range of each species that is not protected under the existing conservation network. This proportion is calculated here by dividing the area of each species distribution that does not fall in a Tier 1/2 area by the total area of the species range. For each 25 m^2 pixel, this species-specific score was then summed across all species present in each pixel to get the total priority scores across the landscape. The analysis was done first with all species distributions and then with only species of conservation concern as they have the greatest need for protection. Species were classified as being of conservation concern if they were threatened (VU, EN, or CR category on the Swiss National Red Lists) or protected by Swiss legislation (see Appendix B).

The Zonation Method uses an algorithm with an iterative ranked cell removal method (Moilanen et al., 2005). The additive benefit function (ABF) was used as the removal rule because it is optimal when the spatial extent of the case study is relatively small when compared to species ranges, and when the goal is conserving overall species richness. In addition, core-area zonation (CAZ) is not recommended when incorporating land costs to an analysis that identifies biologically important areas (Moilanen et al., 2014).

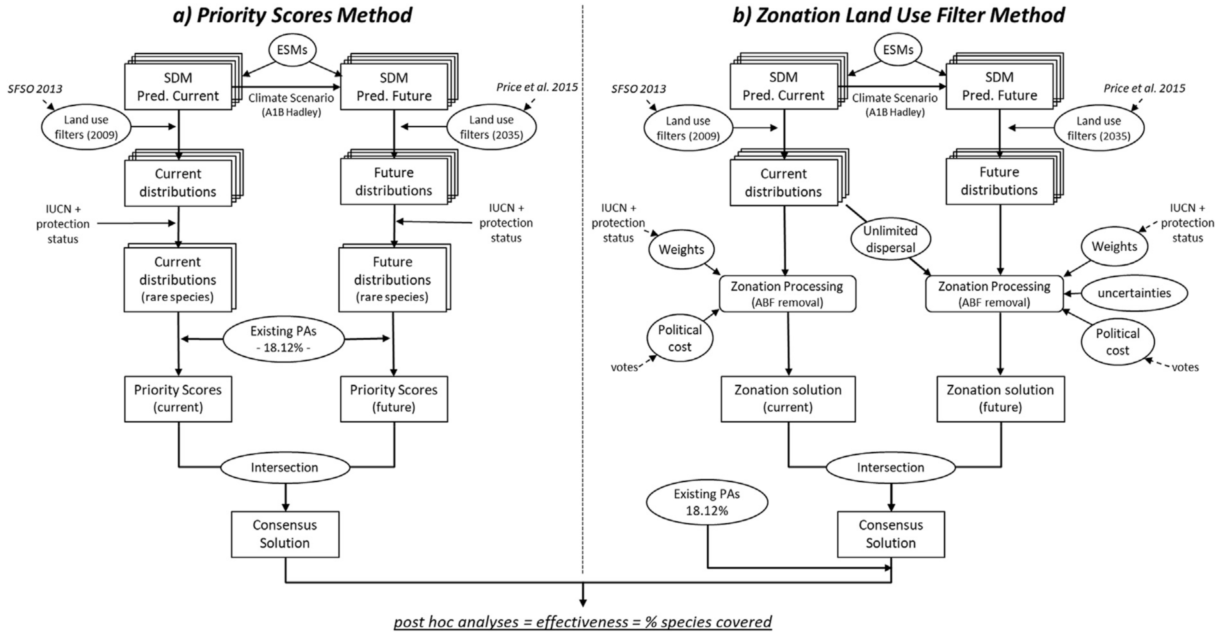

Fig. 2. A schematic representation of the framework used for this analysis: a) the "Priority Scores Method" and b) the "Zonation Land-Use Filter Method", both described in detail in the methods. The Zonation method with the land-use mask and negative weighting differs from the Land-Use Filter Method since it used unfiltered species distributions and excluded urban areas while also negatively weighting less favorable land-use types (not in figure).

Each feature (e.g. species, land-use type) that was added to a Zonation analysis was assigned a weight, and the aggregate weight of features in each cell defines its priority during the cell removal process with a higher weight given a higher priority (Moilanen et al., 2005). In this analysis, species feature weights were first assigned based on species IUCN status with critically endangered species given the highest weight (Appendix B). Uncertainty in the modelling was addressed by giving lower weights to the future species distributions than to the present, and the lowest in the connectivity between these time steps, because future projections carry higher uncertainties (Moilanen et al., 2014).

Zonation solutions were calculated by dividing the total weight of a cell, in this case representing vulnerability-weighted species richness, by the cost associated with protecting that cell. Here, costs were defined as political costs, as calculated by Cardoso (2015), by averaging the opposition results from two referenda on legislation with potentially strong effects on biodiversity conservation. The regions that had higher opposition to beneficial measures for biodiversity were given higher political cost (Fig A2; Appendix A). This was included as it is more difficult to implement changes to expand PAs in regions with higher social opposition to such changes. Monetary costs were not incorporated as they were directly related to land-use.

To prioritize for future distributions under climate change scenarios in the Zonation method, the distribution interaction component of Zonation was used (Moilanen et al., 2014; Rayfield et al., 2009). This provides solutions that transform one conservation target based on its proximity to another represented as an ecological interaction. Here, this was represented as the connectivity of each species distribution between time steps, characterized by the dispersal ability of each species. Engler et al. (2009) found that, for the same study area, simulations of plant distributions with limited dispersal gave similar results to those with unlimited dispersal, being significantly different from those with no dispersal. Therefore, here we only present the results with unlimited dispersal.

Land-use change was added to Zonation by two separate analyses: (i) land-use filter on SDMs (LU-filter; Fig. 2), and (ii) removal mask layer with negative weighting (LU-mask). The LU-filter removed any predicted presence from a land-use type in which no species' observations were recorded. The LU-mask used unfiltered species distributions, excluded urban areas from the analysis using a mask, and negatively weighed other less favorable land-use types. When using future land-use maps for 2035 and climate scenarios to 2060, a conservative estimate of the amount of land-use change predicted in the study area exists.

2.5. Creating consensus solutions and measuring effectiveness

To identify key areas to protect rare species or species with small ranges, we summed the priority scores across all species of conservation concern. Locations with priority scores within the top quartile were selected as priority areas. The current and future scores for species of conservation concern were overlaid to create a consensus map to select the most important areas for conservation.

In the Zonation Method, post-hoc analyses were done automatically in two ways. First, to identify the top 18.12% (same area as the current Tier 1/2 PAs) of the landscape to protect. Second, to assess the effectiveness of both the current Tier 1/2 PAs (included post-hoc as a mask) and the Zonation solutions in protecting modelled species ranges. The Zonation consensus solution is the spatial overlap between current and future proposed networks with the LU-mask method.

3. Results

3.1. Priority scores method

The results from the priority scores follow a similar trend as the diversity maps (Fig A3; Appendix A) and areas with high diversity have higher scores (Fig. 3). Priority scores are predicted to decrease in the future (Fig. 3). The current distributions provide similar priority areas for species of conservation concern as for all species (Fig. 3a and c). The future distributions indicate a mismatch in priority scores between common species and those of conservation concern (Fig. 3b and d). The priority scores differ spatially for different taxa (see Figure A4 and A5; Appendix A). At both time steps, amphibians have high priority near waterways (Fig A4). Reptiles and three insect groups: Hymenopterans (*Bombus* spp.) and Orthopterans have higher priorities at lower elevations (Fig A4, A5), and Lepidopterans at higher elevations (Fig A5).

3.2. Zonation solutions and their effectiveness

The Zonation solutions presented here uses the political land costs, unlimited species dispersal, ABF cell removal rule, and the A1B climate change scenario. The Zonation solutions have over 90% spatial similarity between the land-use methods and the current and future time steps (Fig A6; Appendix A). Although the LU-filter and LU-mask methods protect an almost equal proportion of species distributions (Fig. 4), the LU-filter selects more unfavorable urban areas for converting to PAs. Therefore, the LU-mask was used to create the final solution.

The solutions created by Zonation for the new PA networks performs better than the Tier 1/2 PA at both time steps (Fig. 4). Existing PAs cover on average 25% of all species ranges and new PAs cover an average of 44%. Concerning the future scenario, existing PAs would become less efficient protecting a mean of 23% of a species' range compared with 49% by the new PAs. The existing PAs would protect 23 fewer species than the new PAs (i.e. 23 species would have their range completely outside of the PAs), of which one species is nationally threatened (*Polyommatus damon*, VU), and three are protected by regional or national law (*Traunsteinera globosa*, *Monotropa hypopitys* and *Epipactis purpurata*). The difference in effectiveness between the new and existing PAs is more notable with species of conservation concern (Fig. 4).

3.3. Spatial overlap and final solutions

The composite map of the top priority scores identifies areas at the transition zone between the Rhone valley and the Alps in the South-West of the study area (Fig. 5a). This zone is predominantly south facing dry open grasslands above 1500 m asl. The Zonation consensus solution identifies the areas, selected independently of the existing network, where current and future LU-mask solutions overlap (Fig. 5b). The Zonation solution identifies the same transitional zone as the priority scores as key areas to expand the PA network. However, it also identifies many other areas that the priority scores method omits, predominantly in the South East of the study site, where the Grand Muveran hunting reserve is located.

The supplemental Zonation analyses found that the spatial overlap between new and existing PAs was low, at 34% for current and 32% for future solutions. The analysis found no difference between solutions with unlimited and no dispersal (100% spatial overlap).

4. Discussion

We presented a multi-drivers spatial prioritization method to assess the joint impacts of climate and land-use changes on the optimal locations of nature reserves for the preservation of maximal species richness (of both all modelled species and species with conservation concern) in a mountain region with wide elevational and environmental gradients.

The solutions from the two spatial conservation prioritization schemes used (priority scores and Zonation) suggest that the current PAs are not optimally located to protect high levels of species richness in the Western Swiss Alps. However, some existing PAs were established for other purposes, e.g. the conservation of species-poor habitats such as mires or of specific (e.g. red-listed) species. It is important to note that implementing an optimum PA network might be difficult to achieve, and that simple decision rules (like protecting available sites with the highest species richness) may be more effective in some cases (Meir et al., 2004). PAs are predicted to cover less species richness under future scenarios of climate and land-use change, with 60 of 767 species having their future range outside PAs according to the predicted range shifts. These species might thus face higher threats of local extinction due to habitat fragmentation or degradation outside PAs (Wilcox and Murphy, 1985; Gibson et al., 2011). There is a predicted loss of suitability of the existing PA networks for terrestrial fauna and flora (Araújo et al., 2011; Françoso et al., 2015), but in our study area it is likely stronger due to the mountain landscapes with steep climatic gradients along elevation. This emphasizes the need for using spatial decision support tools for conservation prioritization in areas with steep elevation gradients, like mountains. One limitation of this case study is that it did not

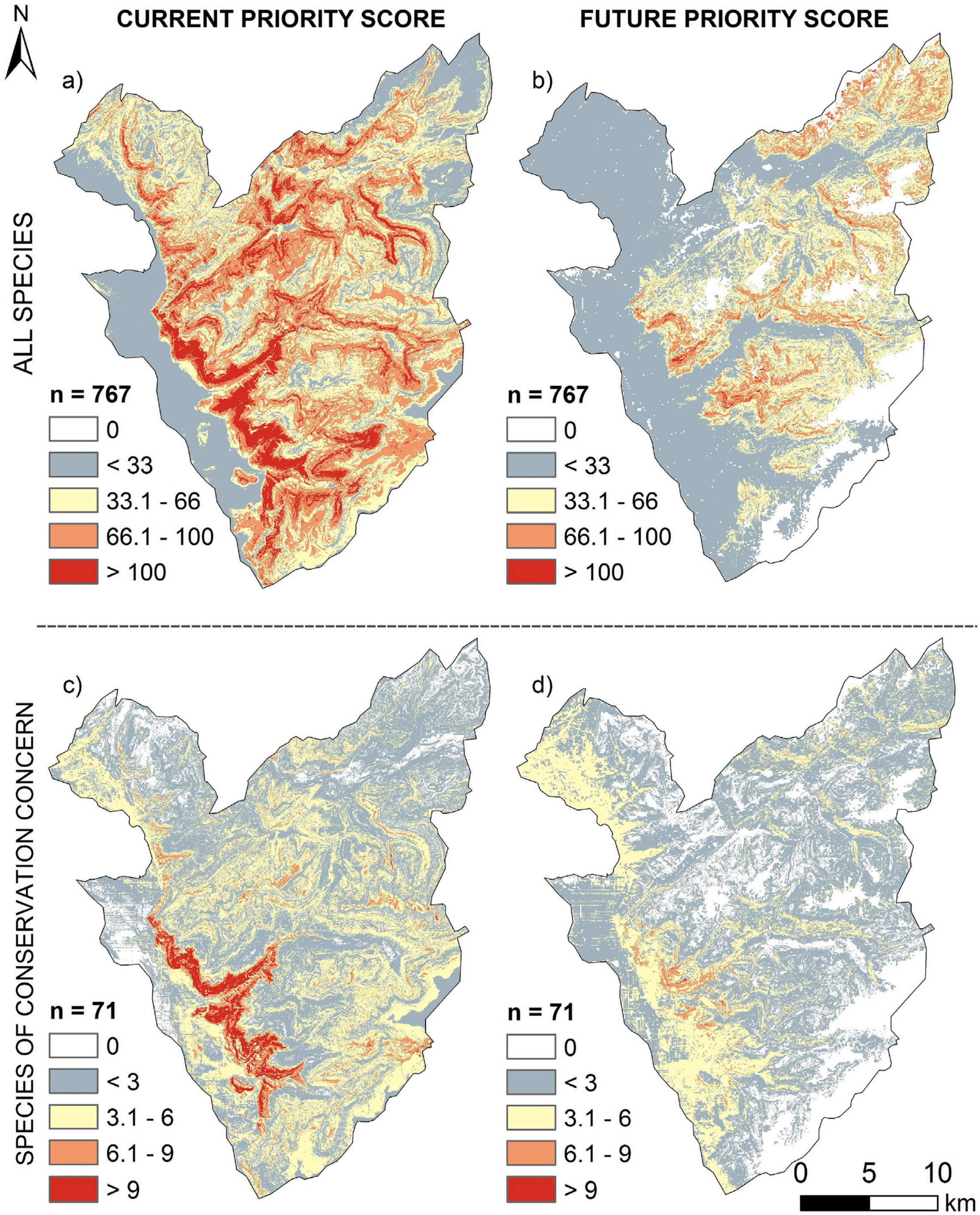

Fig. 3. Priority maps showing the sum of species priority scores of the modelled species with their current (a, c) and projected future (b, d) distributions. Future refers to the distributions predicted to 2060 using the A1B climate change scenario. A subset of the species was used to create maps of species of conservation concern which were identified as being threatened and/or protected (c, d).

account for new species that could colonize the study area following climate change (e.g. from warmer lowland areas in Switzerland, or from outside Switzerland; e.g. Henry et al., 2009; Petitpierre et al., 2016), which could complement species losses within the study area. Because our solutions used the same species pool, this should not affect our comparisons, but future studies using the same framework should include this dimension.

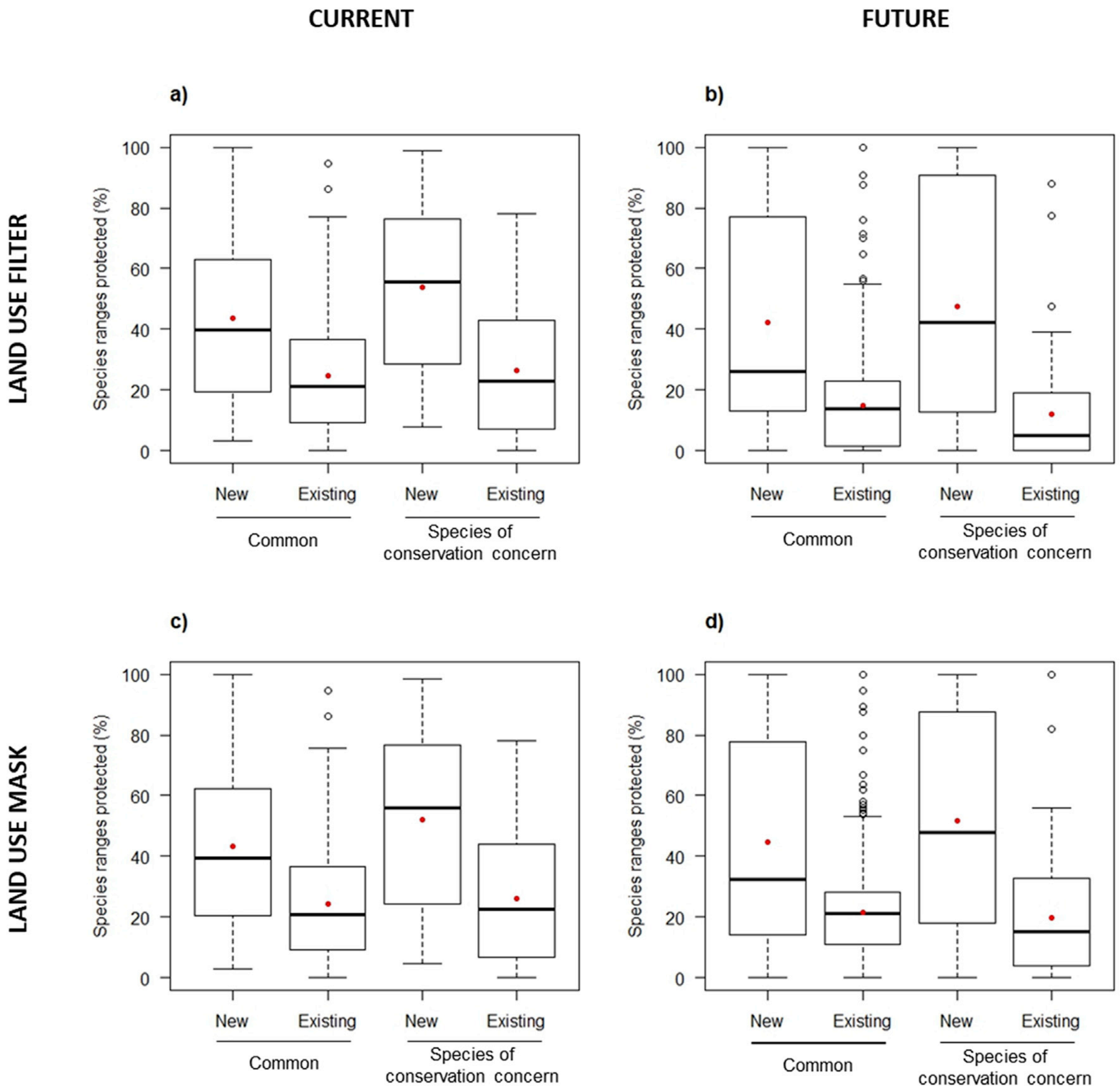

Fig. 4. The proportions of species ranges protected by the Zonation solutions (New) created with LU-filter (a, b) and LU-mask (c, d) compared with the existing protected areas (Existing). Species of conservation concern are all of those listed as threatened and/or protected, and common species are all other species. Future refers to the distributions predicted to 2060 with the A1B climate change scenario. Open circles indicate outliers, black bars show medians, and solid dots indicate means. The same data is subdivided by taxonomic group and can be found in Appendix A (Fig A7).

The priority scores and Zonation methods provide contrasting solutions that can be useful to address different conservation questions. In the case study illustrated here, both methods identified the transition zone between the low elevation flat plain of the Rhone valley and the first slopes of the Alps as a priority area to conserve biodiversity. This zone is predominantly dry grassland, which holds one of the most diverse plant communities among European ecosystems (Janišová et al., 2011). This is likely explained by the high number of plant species used for this analysis as well as our goal of protecting the highest level of species richness from our set of species. The Zonation solution also highlighted the importance of the Grand Muveran faunal reserve (*District Franc Fédéral*) in the south-east of the study area that the priority scores method did not identify. The priority scores method provides solutions that can be more easily implemented as it proposes priority areas to be added to existing networks (Fig. 5a). The Zonation method (Fig. 5b) supplies key regions where human impacts should be minimized, or where future protection should be focused, to maintain high species richness. The results from the priority scores show a mismatch in the priority areas between common species and those of conservation concern. This highlights the importance of setting clear goals with policy makers and scientists before undertaking a similar analysis in other areas (e.g. protecting threatened species versus biodiversity in general; Grant et al., 2013).

Land-use change has only recently been incorporated into Zonation analyses (Faleiro et al., 2013; Struebig et al., 2015; Zwiener et al., 2017; Verhagen et al., 2018). In this work, two methods of accounting for land-use change – LU-filter and LU-

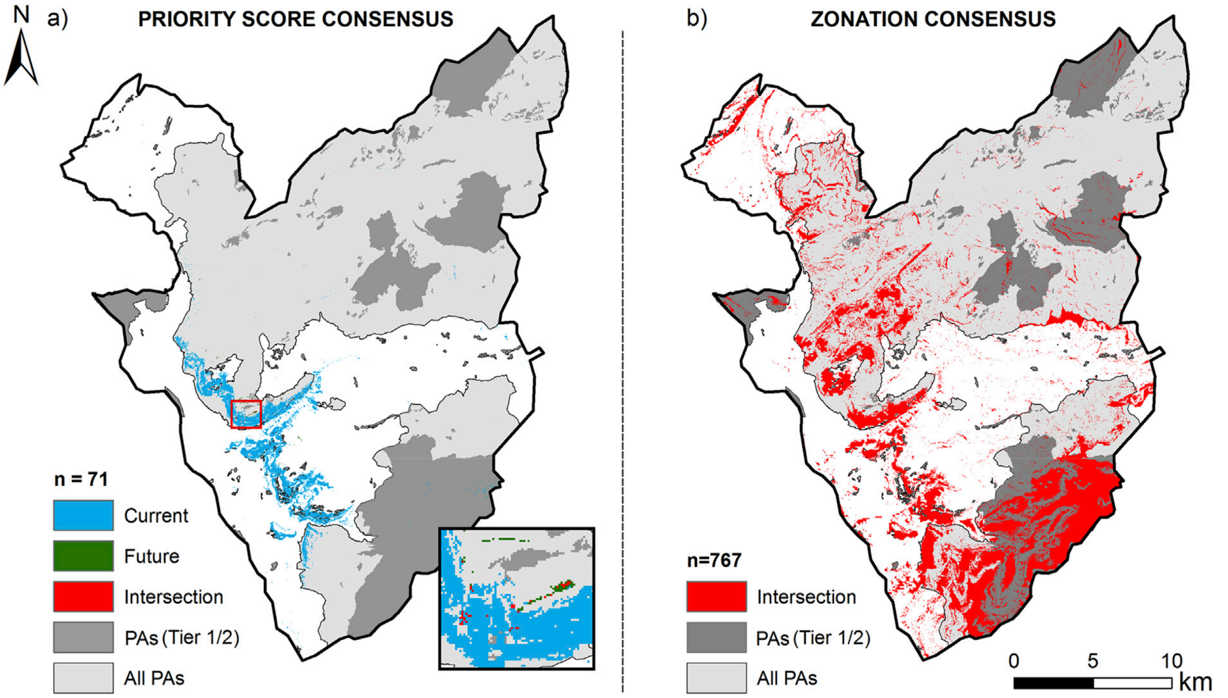

Fig. 5. Final solutions with spatial overlaps (i.e. intersections). a) The priority score consensus solution created by overlaying the current (blue) and future (green) priorities for threatened and/or protected species. The overlapping regions are shown in red and represent areas that are priorities in both time steps (see inset for more detail). b) The Zonation consensus solution created by overlaying the current and future LU-mask solutions. The overlapping regions are also shown in red and represent the areas that are priorities at both time steps. The full extent of protected areas is shaded in light grey (all 4 tiers) and the top two tiers are shaded in dark grey. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

mask – were used. The LU-mask produced solutions for lower conflicts between human uses and biodiversity conservation as urban areas were excluded from solutions. Future analyses could also add other non-convertible lands to this mask (e.g. one might exclude areas where agricultural production is given priority over other uses by the government). Globally, the increasing demand for food by the growing human population (Foley et al., 2011) will likely increase the risk of conflict over land-uses. Because of the trade-off between minimizing conflict and increasing the proportion of species ranges that can be protected, we would recommend combining these land-use methods in future studies by first including a filter and then adding a mask to remove non-convertible lands.

The goal of this analysis was to protect the highest possible level of diversity across all species in the four taxonomic groups and those of conservation concern using decision support tools. Applying these tools towards conservation prioritization appears to be less common in European countries than in more economically developing or biodiversity rich countries (e.g. Brazil, Australia, Madagascar; based on a non-exhaustive bibliographic research done by the authors; e.g. Kremen et al., 2008). This infrequent recourse to spatial decision tools could be due to the well-established (even if insufficient) existing PA network in Europe, likely considered already optimal by the public and governments. However, existing PAs have been more frequently created in places that are unsuitable for economic activities, and not necessarily in areas with high biodiversity (Margules and Pressey, 2000). Human density is high in Europe, creating a trade-off between minimizing conflict and increasing the proportion of species ranges that can be protected. Additionally, it could be due to an emphasis placed on land sharing rather than land sparing in many densely populated countries (Phalan et al., 2011). For example, many European countries use set-asides in agricultural areas to protect biodiversity (Van Buskirk and Willi, 2004). This strategy allows the focus to be on conserving irreplaceability ahead of high biodiversity, highlighting the challenges of conservation and the need to set specific conservation targets.

4.1. Identified gaps, suggestions and ways forward in conservation planning

The study case here examined allows to evidence five important issues that should be fronted to move forward in conservation planning.

First, here we choose to maximize species richness of all species or those of conservation concern. However, other dimensions of biodiversity can be of interest in the considered area or for applications in other spatial contexts. For instance, irreplaceability and complementarity, special habitats (e.g. bogs), functional groups (e.g. national priority species), ecosystem services (i.e. nature's contributions to society; Díaz et al., 2015), and various genetic facets of biodiversity, all could be considered according to the ultimate goal of conservation planning. Similarly, our approach could be expanded to include also other threats to biodiversity, such as biological invasions (Vincente et al., 2013).

Second, we showed our approach by using four taxonomic groups for which data were available, disregarding other charismatic vertebrates, especially mammals and birds, because of lacking adequate spatial information (data were not available with the same coverage, quality or reliability). However, the approach we demonstrated can easily be updated once new data will be available. Future analyses could also differentially weight taxonomic groups based on pre-defined conservation goals.

Third, and still related to data availability, mismatches in the data from different academic fields - such as different spatial and temporal scales for the biological, climate and land-use data and scenarios - can make their joint use in such integrated conservation planning analyses more difficult.

Fourth, by using SDMs, some source of uncertainties cannot be excluded (Barry and Elith, 2006; Rocchini et al., 2011). These will be summed up with uncertainties related to the use of decision tools like Zonation when considering land-use and climate change predictions (Moilanen et al., 2006). To improve our approach in future applications, uncertainty issues within Zonation could be attenuated through distribution discounting (Moilanen et al., 2006), measuring the variance between species distributions predicted from multiple SDMs (Faleiro et al., 2013; Lemes and Loyola, 2013), or by differentially weighing current and future species distribution layers based on uncertainty, as future distributions have higher uncertainty (Kujala et al., 2013). It is also important to evaluate if sufficient data is available for all the species to be used in the analysis (e.g. Canessa et al., 2015) and to test the effects of different thresholds when creating binary distribution data from SDMs (e.g. Fernandes et al., 2018).

Fifth, an important extension of our framework could be the definition of conservation targets in concert with stakeholders: doing so would be crucial in applications aimed to revise PAs network, e.g. in view of new threats or climate change. In this regard, there is still limited communication between science and policy on the use of modelling approaches to support conservation decisions (Guisan et al., 2013; Tulloch et al., 2016). Ideally, scientists, stakeholders and the public would need to come together and share ideas to define targets and achieve a consensus on what might be considered as achievable (Wilson, 2008; Dicks et al., 2014). Improving this science-society link remains especially important to resolve the ‘implementation crisis’ wherein the scientific ability to create these results outweighs the ability to apply them (Knight and Cowling, 2003; Arlettaz et al., 2010). In the study region, a step was already taken in this direction through the implementation of a science-policy ‘forum’ (“*bourses aux questions*”) set-up on the RECHALP web geoportal to support transdisciplinary research in this study area (rechalp.unil.ch). This can be taken as an example to multiply similar initiative for different PA networks.

The framework for conservation prioritization with decision support tools here presented is an improvement upon previous methods of conservation planning, by incorporating data from multidisciplinary sources and by adding data from multiple taxonomic groups at fine resolution in a mountain region. The application of the framework, and potentially the implementation of the above suggestions, could create solutions for future conservation goals both in this region and in other spatial context with similar data. However, its suitability needs to be tested when using different extents or resolutions. Utilizing spatial decision support tools is just one component of conservation planning (Guisan et al., 2013), which also needs to be addressed through policy, education, and economics (Wilson et al., 2005). As species are expected to continually move with global change, setting conservation targets needs to be an adaptive process that will not create one final optimal answer but several dynamic optima, which vary with changing threats and conservation targets (Singh and Milner-Gulland, 2011). A model-based framework, as proposed here, has the additional advantage that it can be implemented in an adaptive manner (Guisan et al., 2006).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00589.

References

Alagador, D., Cerdeira, J.O., Araújo, M.B., 2014. Shifting protected areas: scheduling spatial priorities under climate change. J. Appl. Ecol. 51, 703–713.

Araújo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Glob. Chang. Biol. 10, 1618–1626.
Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecol. Lett. 14, 484–492.
Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M., Braunisch, V., 2010. From publications to public actions: when conservation biologists bridge the gap between research and implementation. Bioscience 60, 835–842.
Barry, S., Elith, J., 2006. Error and uncertainty in habitat models. J. Appl. Ecol. 43, 413–423.
Bosshard, T., Kotlarski, S., Ewen, T., Schär, C., 2011. Spectral representation of the annual cycle in the climate change signal. Hydrol. Earth Syst. Sci. 15, 2777–2788.
Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.
Breiner, F.T., Guisan, A., Bergamini, A., Nobis, M.P., 2015. Overcoming limitations of modelling rare species by using ensembles of small models. Methods in Ecology and Evolution 6, 1210–1218.
Bugmann, H., Gurung, A.B., Ewert, F., Haeberli, W., Guisan, A., Fagre, D., Kaab, A., 2007. Modeling the biophysical impacts of global change in mountain biosphere reserves. Mt. Res. Dev. 27, 66–77.
Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J.J., Southwell, D.M., Armstrong, D.P., Chadès, I., Lacy, R.C., Converse, S.J., 2015. When do we need more data? A primer on calculating the value of information for applied ecologists. Methods in Ecology and Evolution 6 (10), 1219–1228.
Cardoso, A.R.P., 2015. Spatial Data and Modelling for the Prioritisation of Conservation Areas in the Alpine Region of the Canton of Vaud. Master's Thesis. Faculdade de Ciências Sociais e Humanas – Universidade Nova de Lisboa, Portugal.
CBD, 2010. Global Biodiversity Outlook 3. Secretariat of the Convention on Biological Diversity (CBD), Montreal, 94 pp.
Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024–1026.
D'Amen, M., Pradervand, J.-N., Guisan, A., 2015. Predicting richness and composition in mountain insect communities at high resolution: a new test of the SESAM framework: community-level models of insects. Glob. Ecol. Biogeogr. 24, 1443–1453.
Díaz, S., et al., 2015. The IPBES Conceptual Framework — connecting nature and people. Current Opinion in Environmental Sustainability 14, 1–16.
Dicks, L.V., Walsh, J.C., Sutherland, W.J., 2014. Organising evidence for environmental management decisions: a '4S'hierarchy. Trends Ecol. Evol. 29, 607–613.
Dubuis, A., Pottier, J., Rion, V., Pellissier, L., Theurillat, J.-P., Guisan, A., 2011. Predicting spatial patterns of plant species richness: a comparison of direct macroecological and species stacking modelling approaches. Divers. Distrib. 17, 1122–1131.
Engler, R., Randin, C.F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N.E., Guisan, A., 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? Ecography 32, 34–45.
Faleiro, F.V., Machado, R.B., Loyola, R.D., 2013. Defining spatial conservation priorities in the face of land-use and climate change. Biol. Conserv. 158, 248–257.
Fernandes, R.F., Scherrer, D., Guisan, A., 2018. How much should one sample to accurately predict the distribution of species assemblages? A virtual community approach. Ecol. Inf. 48, 125–134.
Fleishman, E., Thomson, J.R., Kalies, E.L., Dickson, B.G., Dobkin, D.S., Leu, M., 2014. Projecting current and future location, quality, and connectivity of habitat for breeding birds in the Great Basin. Ecosphere 5, 1–29.
Foley, J.A., et al., 2011. Solutions for a cultivated planet. Nature 478, 337.
Françoso, R.D., Brandão, R., Nogueira, C.C., Salmona, Y.B., Machado, R.B., Colli, G.R., 2015. Habitat loss and the effectiveness of protected areas in the Cerrado Biodiversity Hotspot. Natureza & Conservação 13, 35–40.
Gibson, L., et al., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.
Grant, E.H.C., Zipkin, E.F., Nichols, J.D., Campbell, J.P., 2013. A strategy for monitoring and managing declines in an amphibian community. Conserv. Biol. 27, 1245–1253.
Guisan, A., Broennimann, O., Engler, R., Vust, M., Yoccoz, N.G., Lehmann, A., Zimmermann, N.E., 2006. Using niche-based models to improve the sampling of rare species. Conserv. Biol. 20, 501–511.
Guisan, A., et al., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16, 1424–1435.
Guisan, A., Thuiller, W., Zimmermann, N.E., 2017. Habitat Suitability and Distribution Models. Cambridge University Press, Cambridge, UK.
Guisan, A., et al., 2019. Climate change impact on mountain biodiversity. In: Lovejoy, T.E., Hannah, L. (Eds.), Climate Change & Biodiversity, second ed. Yale University Press (in press).
Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142, 14–32.
Henry, P., Le Lay, G., Goudet, J., Guisan, A., Jahodová, Š., Besnard, G., 2009. Reduced genetic diversity, increased isolation and multiple introductions of invasive giant hogweed in the western Swiss Alps. Mol. Ecol. 18, 2819–2831.
Hickling, R., Roy, D.B., Hill, J.K., Fox, R., Thomas, C.D., 2006. The distributions of a wide range of taxonomic groups are expanding polewards. Glob. Chang. Biol. 12, 450–455.
IPCC, 2001. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), Climate Change 2001: the Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, p. 88.
Janišová, M., Bartha, S., Kiehl, K., Dengler, J., 2011. Advances in the conservation of dry grasslands: introduction to contributions from the seventh European dry grassland meeting. Plant Biosyst. 145 (3), 507–513.
Jenkins, C.N., Houtan, K.S.V., Pimm, S.L., Sexton, J.O., 2015. US protected lands mismatch biodiversity priorities. Proc. Natl. Acad. Sci. Unit. States Am. 112, 5081–5086.
Knight, A.T., Cowling, R.M., 2003. Conserving South Africa's "Lost" Biome: a Framework for Securing Effective Regional Conservation Planning in the Subtropical Thicket Biome. TERU Report No. 44. Terrestrial Ecology Research Unit, University of Port Elizabeth, South Africa.
Kremen, C., Cameron, A., Moilanen, A., Phillips, S., Thomas, C., Beentje, H., Dransfield, J., Fisher, B., Glaw, F., Good, T., 2008. Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. Science 320, 222–226.
Kujala, H., Moilanen, A., Araújo, M.B., Cabeza, M., 2013. Conservation planning with uncertain climate change projections. PLoS One 8 (2) e53315.
Lambin, E.F., et al., 2001. The causes of land-use and land-cover change: moving beyond the myths. Glob. Environ. Chang. 11, 261–269.
Lemes, P., Loyola, R.D., 2013. Accommodating species climate-forced dispersal and uncertainties in spatial conservation planning. PLoS One 8 (1) e54323.
Liu, C.R., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.
Lomba, A., Pellissier, L., Randin, C., Vicente, J., Moreira, F., Honrado, J., Guisan, A., 2010. Overcoming the rare species modelling paradox: a novel hierarchical framework applied to an Iberian endemic plant. Biol. Conserv. 143, 2647–2657.
Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.
McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models, second ed. CRC Press.
Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecol. Lett. 7, 615–622.
Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Synthesis. Island Press, Washington, DC.
Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing multiple-use landscapes for conservation: methods for large multi-species planning problems. Proc. R. Soc. Lond. B Biol. Sci. 272, 1885–1891.
Moilanen, A., Wintle, B.A., Elith, J., Burgman, M., 2006. Uncertainty analysis for regional-scale reserve selection. Conserv. Biol. 20, 1688–1697.
Moilanen, A., Pouzols, F.M., Meller, L., Veach, V., Arponen, A., Leppänen, J., Kujala, H., 2014. Zonation Spatial Conservation Planning Methods and Software. Version 4. User Manual. University of Helsinki, Finland.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends Ecol. Evol. 21, 681–687.
Newburn, D., Reed, S., Berck, P., Merenlender, A., 2005. Economics and land-use change in prioritizing private land conservation. Conserv. Biol. 19, 1411–1420.
Petitpierre, B., McDougall, K., Seipel, T., Broennimann, O., Guisan, A., Kueffer, C., 2016. Will climate change increase the risk of plant invasions into mountains? Ecol. Appl. 26, 530–544.
Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333, 1289–1291.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modelling of species geographic distributions. Ecol. Model. 190, 231–259.
Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.
Pouzols, F.M., Toivonen, T., Di Minin, E., Kukkala, A.S., Kullberg, P., Kuusterä, J., Lehtomäki, J., Tenkanen, H., Verburg, P.H., Moilanen, A., 2014. Global protected area expansion is compromised by projected land-use and parochialism. Nature 516, 383–386.
Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K.A., 2007. Conservation planning in a changing world. Trends Ecol. Evol. 22, 583–592.
Price, B., Kienast, F., Seidl, I., Ginzler, C., Verburg, P.H., Bolliger, J., 2015. Future landscapes of Switzerland: risk areas for urbanisation and land abandonment. Appl. Geogr. 57, 32–41.
Randin, C.F., Dirnböck, T., Dullinger, S., Zimmermann, N.E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? J. Biogeogr. 33, 1689–1703.
Rayfield, B., Moilanen, A., Fortin, M.-J., 2009. Incorporating consumer-resource spatial interactions in reserve design. Ecol. Model. 220, 725–733.
Rocchini, D., Hortal, J., Lengyel, S., Lobo, J.M., Jimenez-Valverde, A., Ricotta, C., Bacaro, G., Chiarucci, A., 2011. Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. Prog. Phys. Geogr. 35, 211–226.
Scherrer, D., Massy, S., Meier, S., Vittoz, P., Guisan, A., 2017. Assessing and predicting shifts in mountain forest composition across 25 years of climate change. Divers. Distrib. 23, 517–528.
Scherrer, D., Mod, H.K., Pottier, J., Litsios-Dubuis, A., Pellissier, L., Vittoz, P., Götzenberger, L., Zobel, M., Guisan, A., 2019. Disentangling the processes driving plant assemblages in mountain grasslands across spatial scales and environmental gradients. J. Ecol. 107, 265–278. https://doi.org/10.1111/1365-2745.13037.
SFSO, Swiss Federal Statistical Office, 2013. Land use in Switzerland: results of the Swiss land use statistics. Neuchatel.
Singh, N.J., Milner-Gulland, E.J., 2011. Conserving a moving target: planning protection for a migratory species as its distribution changes: landscape-scale planning for a migratory species. J. Appl. Ecol. 48, 35–46.
Steffen, W., Crutzen, P.J., McNeill, J.R., 2007. The Anthropocene: are humans now overwhelming the great forces of nature. AMBIO A J. Hum. Environ. 36, 614–621.
Struebig, M.J., et al., 2015. Targeted conservation to safeguard a biodiversity hotspot from climate and land-cover change. Curr. Biol. 25, 372–378.
Summers, D.M., Bryan, B.A., Crossman, N.D., Meyer, W.S., 2012. Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. Glob. Chang. Biol. 18, 2335–2348.
Tulloch, A.I.T., Sutcliffe, P., Naujokaitis-Lewis, I., Tingley, R., Brotons, L., Ferraz, K.M.P.M.B., Possingham, H., Guisan, A., Rhodes, J.R., 2016. Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. Biol. Conserv. 199, 157–171.
Van Buskirk, J., Willi, Y., 2004. Enhancement of farmland biodiversity within set-aside land. Conserv. Biol. 18 (4), 987–994.
Verburg, P.H., Overmars, K.P., 2009. Combining top-down and bottom-up dynamics in land use modeling: exploring the future of abandoned farmlands in Europe with the Dyna-CLUE model. Landsc. Ecol. 24, 1167–1181.
Verhagen, W., van Teeffelen, A.J.A., Verburg, P.H., 2018. Shifting spatial priorities for ecosystem services in Europe following land use change. Ecol. Indicat. 89, 397–410.
Vincente, J.R., Fernandes, R.F., Randin, C.F., Broennimann, O., Goncalves, J., Marcos, B., Pocas, I., Alves, P., Guisan, A., Honrado, J.P., 2013. Will climate change drive alien invasive plants into areas of high protection value? An improved model-based regional assessment to prioritise the management of invasions. J. Environ. Manag. 131, 185–195.
Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.
Wan, J., Wang, C., Yu, J., et al., 2016. Developing conservation strategies for *Pinus koraiensis* and *Eleutherococcus senticosus* by using model-based geographic distributions. J. For. Res. 27, 389–400.
Welch, D., 2005. What should protected area managers do in the face of climate change. George Wright Forum 22, 75–93.
Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. Am. Nat. 125, 879–887.
Wilson, K., Pressey, R.L., Newton, A., Burgman, M., Possingham, H., Weston, C., 2005. Measuring and incorporating vulnerability into conservation planning. Environ. Manag. 35, 527–543.
Wilson, R.S., 2008. Balancing emotion and cognition: a case for decision aiding in conservation efforts. Conserv. Biol. 22, 1452–1460.
Zhang, K., Laffan, S.W., Ramp, D., et al., 2011. Incorporating a distance cost in systematic reserve design. Int. J. Geogr. Inf. Sci. 25, 393–404.
Zwiener, V.P., Padial, A.A., Marques, M.C.M., Faleiro, F.V., Loyola, R., Peterson, A.T., 2017. Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest. Divers. Distrib. 23, 955–966.