# Modelling the habitat selection of the bearded vulture to predict areas of potential conflict with wind energy development in the Swiss Alps

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## ABSTRACT

Global warming impels countries to dramatically reduce their release of greenhouse gas emissions and increase their reliance on green energy, notably wind power. Yet, without cautious planning, the sprawl of wind turbines could negatively impact biodiversity, especially flying vertebrates that are otherwise already threatened. Inherent risks for vulnerable and endangered species are usually mitigated by banning constructions within buffer areas around nesting locations. This approach, however, neglects species' range dynamics and particularly falls short of protecting expanding populations, as in the case of natural returns or reintroduction programmes. We present here an alternative approach to mitigate wildlife-infrastructure conflicts, applying it to the bearded vulture, a species reintroduced in the European Alps. Combining casual observations and GPS locations of tagged individuals, we built several predictive distribution models with respect to bearded vulture age class and season and tested for models' ability to correctly predict its future expansion in the Alps. Although immature and adult birds showed different habitat selection patterns, both in summer and winter, wide areas of the Swiss Alps (40%) offer suitable habitat. The above combined information enabled correctly predicting today's use by breeding bearded vultures of previously unused areas. This study not only provides a detailed analysis of the bearded vulture's ecological requirements in the Alps but also helps delineating areas where conflicts with wind energy production and other aerial infrastructure will likely occur in Switzerland. The resulting maps provide a large-scale planning tool that companies, landscape planners and wildlife managers can use in any environmental risk assessments.

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## 1. Introduction

Climate change and the increase in energy demand are leading to a progressive shift towards fossil-free energy production worldwide. With the Paris Climate Agreement ratified in 2015, nations have agreed to diminish global warming by adopting several measures, notably increasing the share of their total energy consumption with at least 20% renewable energy. Among the available renewable energy sources, wind power has developed rapidly during the last decades (Leung and Yang, 2012) and is now playing a key role in the energy transition, having reached a worldwide capacity of 651 GW in 2019 (Lee and Zhao, 2020).

Although wind energy does not release greenhouse gases into the atmosphere, wind turbines can have a negative impact on wildlife, especially on flying vertebrates, i.e. bats (Arnett et al., 2015; Rydell et al., 2010) and birds (Barrios and Rodríguez, 2004; Carrete et al., 2009). The main negative effects are mortality resulting from collisions with rotor blades and related power lines, and displacement caused by disturbance or habitat loss (Drewitt and Langston, 2006; Madders and Whitfield, 2006). Large soaring raptors are highly affected by collisions (Carrete et al., 2009; Dahl et al., 2012; de Lucas et al., 2012; Ferrer et al., 2012; Katzner et al., 2017). Possible explanations include: 1) a low reproductive rate which, usually combined with a late sexual maturity, makes each additional source of mortality detrimental (Beston et al., 2016; Carrete et al., 2009; Watson et al., 2018), 2) a limited visual field in the direction of movement, which reduces the perception of vertical obstacles ahead (Martin et al., 2012), and 3) the fact that the wind industry often deploys on areas with landforms and wind conditions similar to those selected by raptor species (Katzner et al., 2012; Poessel et al., 2018; Rushworth and Krüger, 2014). Collision with wind turbines is thus considered a major or even critical threat for some vulture species (Botha et al., 2017).

Vultures represent a highly vulnerable ecological guild (Buechley and Şekercioğlu, 2016). Their populations have steadily and dramatically declined over the last few decades in many regions (Ogada et al, 2012, 2016; Safford et al., 2019), with few exceptions (e.g. griffon vulture (*Gyps fulvus*) in Western Europe (Safford et al., 2019)). Conservation action has thus been taken to avoid global or local extinction of many vulture species. For example, the withdrawal of diclofenac as veterinary drug prevented a further decline of vultures in India, Nepal and Pakistan (Cuthbert et al., 2011; Galligan et al., 2014; Prakash et al., 2012) while a release programme was necessary to save the California condor (*Gymnogyps californianus*) from extinction in North America (Walters et al., 2010). Other reintroduction programmes were initiated in Europe to reinstate or reinforce vulture populations, including the cinereous vulture (*Aegypius monachus*) in France (Eliotout et al., 2007) and Bulgaria (Stoynov et al., 2019), and the griffon vulture in Southern France (Sarrazin et al., 1994), in the Balkans (Demerdzhiev et al., 2014; Stoynov et al., 2018), in Sardina (Italy, Aresu et al., 2020) and in Cyprus. The bearded vulture (*Gypaetus barbatus*) was similarly reintroduced into the European Alps (Robin et al., 2004; Schaub et al., 2009).

The massive expansion of the wind industry in recent times represents a new rapidly growing source of threat for vultures and other raptors, which calls for a meticulous spatial planning of wind plants deployment. In Europe, the precautionary principle is usually applied to protect endangered species potentially affected by wind turbine infrastructure (Braunisch et al., 2015; Kriebel et al., 2001). This typically results in wind turbines being excluded from buffer areas around sensitive locations, principally nesting sites, with buffer radii defined based on expert knowledge or estimated according to species' home range size (Bright et al., 2008; Janss et al., 2010; Venter et al., 2019). However, this approach is limited and cannot safely protect the populations of vulnerable species for several reasons. Firstly, it is static. As it is based on the extant knowledge at a specific point of time, it inherently lacks predictive power and thus cannot address nor anticipate future conflicts, which is especially problematic for highly dynamic, expanding or declining populations (Braunisch et al., 2015). Secondly, it normally accounts for habitat selection at one life stage, namely breeding, but species could use habitats diversely at different life stages or times of the year (Hirzel et al., 2004; Krüger et al., 2014). Spatial and temporal variations in occurrence probability are thus usually not considered, with potentially dramatic consequences for both collision-prone species and wind energy planners: expanding populations may lose potentially suitable habitat while planners may face new, unforeseen restrictions because an endangered species suddenly appears in an area that had been pre-selected for a wind farm while the species was not yet inhabiting it. This may particularly be the case for reintroduced species that have not yet re-colonized parts of their historical distribution range. A good planning instrument identifying areas of actual and future potential conflict with wind turbine installations and other aerial infrastructures should be able to predict future circumstances and incorporate information on species' ecological requirements at different life stages and times of the year.

In our study, we focused on season and age-related variations in habitat selection of an endangered vulture species, the bearded vulture, a long-lived cliff-nesting bird that was extirpated from many European countries at the beginning of the 20 century (Mingozzi and Estève, 1997). An ambitious large-scale reintroduction programme started in 1978 to reinstate bearded vulture populations in the Alpine arc. Releases of juvenile birds began in Austria as early as 1986 (Frey and Walter, 1989), and continued regularly in three additional countries: continental France (1987), Italy and Switzerland (1991), with more recent reintroductions in Spain (2006) and Corsica (2016). Since 1986, 227 individuals have been released from a captive population while 272 chicks naturally fledged in the wild in the Alps, all the latter originally stemming from reintroduced ancestors. If Schaub et al. (2009) evidenced a high annual survival probability for the Alpine population (ca 0.88 during the first year, 0.96 afterwards), they feared that a 50% increase in the annual mortality rate would result in a population decline (Schaub et al., 2009). This means that even a few additional fatalities per year, as feared with the ongoing and future expansion of wind turbines throughout the Alps, would reverse the steady population growth and jeopardize this long-term reintroduction program whose success has been so inspirational.

Regarding species' ecological requirements in the Alpine range, if Hirzel et al. (2004) already distinguished two different age classes: juveniles/immatures (i.e. individuals typically in an exploring phase) and subadults/adults (phase of territory settlements), their model was restricted to an area of 5200 km$^2$ in the SW Swiss Alps and did not account for seasonality. The present model is not only based on much more information, including GPS tracked individuals in addition to casual observations, but it encompasses the whole Swiss Alps and considers two time-periods. Its objective is also not only to predict habitat suitability throughout the Swiss Alps but also to properly evaluate the models' potential to predict the future spatial expansion of the spreading Alpine bearded vulture population from a conservation perspective. In effect, identifying broad-scale areas that are — and will be — potentially suitable for the species in the Alps is the only way to prevent conflicts with the development of wind energy and other aerial infrastructures.

## 2. Methods

### 2.1. Study area and species

The study area encompassed the entire Swiss Alpine range (Fig. 1), covering 25,808 km$^2$, which represents about 13.4% of the total area of the Alpine massif (192,753 km$^2$). Four of the six biogeographical regions present in Switzerland (Gonseth et al., 2001) were included: Northern Alps, Inner Western Alps, Inner Eastern Alps, and Southern Alps. Elevation ranges from 191 to 4611 m a.s.l., with an average of ca 1720 m a.s.l. The area is characterized by highly heterogeneous climate conditions, with an oceanic climate in the Northern Alps, continental and subcontinental conditions in the Inner Alps, and Insubric climate in the Southern Alps. The variety of climate conditions together with variegated geological substrates lead to a fairly inhomogeneous landscape across the study area. Since the beginning of the reintroduction programme, the bearded vulture population has been steadily increasing within the Swiss Alpine range. After first successful reproductions in 2007 in both the Western and Eastern Swiss Alps (Biollaz et al., 2011), the number of breeding pairs has increased to 21 breeding territories in 2019. The bearded vulture is a long-lived species characterized by a low fecundity rate (clutch size of two eggs with obligate siblicide) (Margalida et al, 2003, 2004; Schaub et al., 2009) and a delayed age at first successful breeding (on average 11.4 years in the Pyrenees) (Antor et al., 2007). It feeds mostly on bones (Margalida and Villalba, 2017). It is listed as critically endangered in Switzerland (Keller V., Gerber A., Schmid H., Volet B., 2010) and vulnerable in Europe (BirdLife International, 2015).
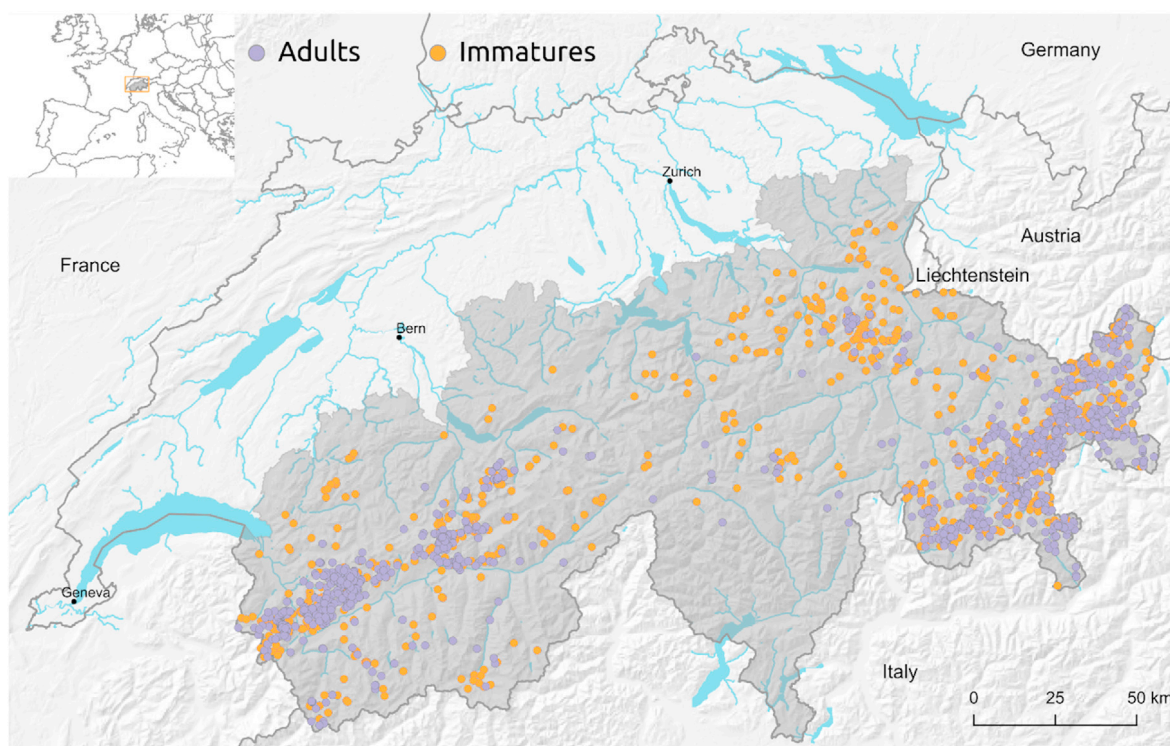


**Fig. 1.** Map of the study area (grey shaded) that encompasses the whole Swiss Alps, with casual observations of adult (violet) and immature (orange) bearded vultures between 2004 and 2014 (unfiltered datasets). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

## 2.2. Environmental predictors

Environmental predictors were chosen based on extant literature (e.g. Hirzel et al., 2004) and ecological knowledge of the species. The original data sources consisted of digital maps in a vector or raster format. Vector data were first converted into raster data with 25 m spatial resolution. Given that the bearded vulture habitat selection is probably driven by habitat quality over a vast area, we accounted for the conditions within a circular moving window of 564 m radius (i.e. 1 km$^2$), corresponding to the sight-field scale of the species (Hirzel et al., 2004), by calculating the average (continuous variables) or the proportion (Boolean variables) within this range. The resulting raster maps were then resampled at 100 m spatial resolution. In that way we compiled a total of 31 environmental variables that can be grouped into six categories: 1) climate, 2) topography, 3) food availability, 4) geological substrate, 5) anthropogenic infrastructure, and 6) land cover and land use (Table 1). Solar radiation was calculated with the Area Solar Radiation tool available in the ArcGIS software version 10.2, taking 2009 as reference year. Chamois and ibex occurrence probabilities were modelled with Maxent version 3.4.1 (Phillips et al, 2006, 2017) (see supplementary material) and used directly as proxies for the potential availability of chamois and ibex carcasses. Sheep and goat densities were estimated by dividing the number of sheep and goats occurring in each community (taken as the average stock size between 2004 and 2014) by the area of alpine pastures present on the territory of the same community.

## 2.3. Data on wind turbines

Locations of operational wind turbines were gathered from the inventory provided by the Swiss Federal Office of Energy (Bundesamt für Energie BFE, 2014). We considered only tall wind plants within the study area, excluding small wind turbines (hub height 9−26 m, blade diameter 4−18 m) as risks of collision with low rotors is unlikely for this species. An additional

**Table 1**
Environmental predictors used for the analysis of the bearded vulture potential distribution across the Swiss Alps with unit of measurement, abbreviation and data source (warm season: May to October; cold season: November to April).

| Category | Description | Unit | Abbreviation | Source |
|---|---|---|---|---|
| Climate | Average precipitation in the cold season | mm | prec122 | WSL[a] |
| | Average precipitation in the warm season | mm | prec57 | WSL |
| | Average solar radiation in the cold season | WH/m$^2$ | solar_rad122 | DHM[b] |
| | Average solar radiation in the warm season | WH/m$^2$ | solar_rad57 | DHM |
| | Average temperature in the cold season | °C | temp122 | WSL |
| | Average temperature in the warm season | °C | temp57 | WSL |
| | Average wind speed at 100 m above ground | m/s | windspeed100 | BFE[c] |
| Topography | Sine of the aspect | −1 to 1 | eastness | DHM |
| | Cosine of the aspect | −1 to 1 | northness | DHM |
| | Standard deviation (SD) of the altitude | m | roughness | DHM |
| | Slope | degree | slope | DHM |
| | Topographic Position Index[d] | Index | tpi | DHM |
| Food | Ibex occurrence probability | 0 to 1 | ibex | CSCF[e] |
| | Chamois occurrence probability | 0 to 1 | chamois | CSCF |
| | Sheep and goat warm season density | N/ha | sheep_goat | BsF[f] |
| Geology | Limestone frequency | % | limestone | GeoKarten500[g] |
| | Gneiss frequency | % | gneiss | GeoKarten500 |
| | Granite frequency | % | granite | GeoKarten500 |
| | Other rock frequency[h] | % | other_rocks | GeoKarten500 |
| Anthropogenic | Distance from skilifts | m | skilift_d | Vector 25[i] |
| | Distance from cableways, not including ski-lifts | m | cableway_d | Vector 25 |
| | Distance from roads and railways | m | road_rail_d | Vector 25 |
| Land cover | Bush frequency | % | bush | Vector 25 |
| | Forest frequency | % | forest | Vector 25 |
| | Glacier frequency | % | glacier | Vector 25 |
| | Marshland frequency | % | marsh | Vector 25 |
| | Grassland and unproductive vegetation frequency | % | other_veg | Vector_25 + BsF |
| | Permanent culture frequency | % | permanent | Vector 25 |
| | Rock frequency | % | rock | Vector 25 |
| | Scree frequency | % | scree | Vector 25 |
| | Distance from lakes and rivers | m | water_d | Vector 25 |

[a] Federal Institute for Forest, Snow and Landscape Research WSL; available upon request: www.wsl.ch.
[b] Digital Height Model of Switzerland (Swisstopo): https://shop.swisstopo.admin.ch/en/products/height_models/dhm25.
[c] Swiss Wind Atlas (Bundesamt für Energie BFE, 2016).
[d] Topographic position index according to Wilson (1984).
[e] Centre suisse de cartographie de la faune (CSCF): http://www.cscf.ch/cscf/de/home.html.
[f] Federal Administration for Statistic Switzerland (BsF): https://www.bfs.admin.ch/bfs/de/home/statistiken.html.
[g] Geo Maps: https://shop.swisstopo.admin.ch/de/products/maps/geology/GK500.
[h] This environmental predictor includes gravels, sands, marl, conglomerate, and sandstone.
[i] Digital Cartographic Model of Switzerland (Swisstopo): https://shop.swisstopo.admin.ch/en/products/maps/national/vector/smv25.

dataset with the planned wind turbines was provided by the Swiss Foundation for Landscape Protection ("Windparkkarte Schweiz - Stiftung Landschaftsschutz Schweiz," n.d.).

### 2.4. Species data

Three different data sources were used for the analyses: casual observations, locations collected by birds tagged with Global Position System (GPS) devices, and nesting site locations. Casual observations, collected across the entire Swiss Alps between 2004 and 2014, were used to model the potential distribution of the bearded vulture. However, such observations, obtained without systematic sampling schemes, might suffer from a sampling bias towards easily accessible areas (Fourcade et al., 2014) and we had to account for it. Several techniques, usually referred to as thinning or filtering, have been successfully adopted to reduce the effect of sampling bias (Aiello-Lammens et al., 2015; Varela et al., 2014), but their application cannot be generalized to all datasets. The best way to assess if the application of a given filter to the data improves the model performance is to train a model with filtered data and evaluate it against an independent, systematically collected dataset (Boria et al., 2014). We therefore used GPS locations from tagged bearded vultures, which can be considered free from any bias, to evaluate different filtering methods applied to the casual observations. Moreover, the dataset containing the precise location of all known nesting sites in 2019 (irrespective of breeding success that year) was used to verify if our models, trained using the casual observations from 2004 to 2014, could correctly identify breeding areas that established after this period.

#### 2.4.1. Casual observations

Observations of bearded vulture were obtained from two databases: IBM (International Bearded Vulture Monitoring) and Ornitho.ch. IBM collects all the observations of the species in an international framework, coordinating the monitoring activities of the different partners of the reintroduction project. In its database are entered only observations which have been verified by local coordinators. Ornitho.ch is the Swiss birding online platform, into which amateur bird watchers and professional ornithologists enter their observation data. Each of the retrieved bearded vulture observations (N = 3890) included date, precise location and photographs of the bird. The portraits were inspected to determine bird's age and accordingly classify the observations into two age classes: juveniles/immatures and subadults/adults. Juveniles/immatures included all individuals with a maximum age of three years (i.e. dark-brownish head and plumage, hereafter referred to as immatures), subadults/adults all older individuals (i.e. light colored head and underparts, hereafter referred to as adults). Moreover, we distinguished between observations collected during the warm season (May–October) and observations collected during the cold season (November–April), producing a total of four distinct datasets that were analyzed separately. For each dataset, we randomly retained only one observation per 100 × 100 m raster pixel (hereafter referred to as unfiltered dataset, Fig. 1) to which different filtering methods were then applied.

#### 2.4.2. GPS data

Within the alpine reintroduction programme framework, 81 captive-bred, young bearded vultures equipped with a GPS device were released since 2005. The GPS tag was fixed with a leg loop harness that included a weak breaking point (Hegglin et al., 2004). In addition, 10 wild-hatched fledglings (in 2016–2019) and one adult bird (2017) were tagged with the same method. All GPS data collected between 2004 and 2014 were from immatures. Therefore, assuming that the casual observations of adult bearded vultures are affected by the same sample bias as that of immature birds, we tested the different filtering techniques on the GPS locations of immatures, and then applied the best performing filter to the adult dataset. As we were not only interested in knowing the accuracy of contemporary models but also of their ability to predict future circumstances, we split the GPS positions into two time frames: fixes collected from 2004 to 2014, covering the same time period as casual observations, and fixes collected between 2015 and 2019, during which the species had been expanding into new areas not previously occupied. For this second time frame, GPS data from adults were also available (i.e. the adult tagged in 2017 and nine tags active for more than 36 months) and therefore tested in our final models.

The GPS data were prepared as follows: 1) for each tagged bird we excluded all the GPS fixes recorded during the first eight weeks, to limit the bias in favor of the releasing or nesting site; 2) all GPS positions collected outside of the Swiss study area, i.e. abroad, were excluded; 3) a subsample of two observations per month was randomly extracted from the remaining locations (we opted for two observations in order to obtain an amount of records comparable with the testing dataset held apart from the casual observations, see Table 3); 4) we merged the subsamples generated from each bird and randomly retained only one observation per raster pixel. This process was repeated for each season, age, and time frame, generating six datasets (warm and cold seasons for immatures during 2004–2014, and for immatures and adults during 2015–2019).

### 2.5. Filtering procedure

In order to identify the best filter type and intensity for our observation datasets, we tested two different techniques, namely the geographic filter (Aiello-Lammens et al., 2015), which selects only one location within a predefined geographic distance, thereby removing spatial clumping, and the environmental filter (Varela et al., 2014), which subdivides the environmental gradient (e.g. of potentially bias-prone variables) into regular bins and selects only one location per bin, thereby reducing clumped samples in particular environmental conditions. Each filtering method was applied with three different intensity levels (i.e. geographic filter: different radii; environmental filter: different bin sizes). The geographic filter was

performed using the function *thin* implemented in the *spThin* R package (Aiello-Lammens et al., 2019), and testing distances equal to 250, 500, and 1000 m. We tested two environmental filters, one built following the recommendation of Castellanos et al. (2019) using the first two Principal Component axes derived from all environmental variables used in our study as environmental gradients, and the other built using the distance from roads and the distance from cableways/ski-lifts, two variables defining site-accessibility in the Alps and thus hypothesized to affect sampling intensity. Both environmental filters were applied dividing the range of their variables into 200, 100, and 80 equal-sized bins. This way we tested a total of nine filters in addition to the unfiltered dataset. The filtering methods were tested separately for the warm and the cold seasons, as mountain regions are less accessible during winter due to the harsh conditions (i.e. low ambient temperature, strong wind and deep snow cover), with the sampling bias changing accordingly. The performance of each filter was finally evaluated with the independent datasets generated from GPS locations using the area under the receiver operating characteristic (ROC) curve (AUC) (Fielding and Bell, 1997).

## 2.6. Modelling approach

Since 1986, the first year with releases, the bearded vulture is recolonizing the Alpine range from the few sites of reintroduction scattered across the massif. In this context, data on species absence are unreliable (in terms of reflecting habitat unsuitability) given that in the future the species will probably settle in areas that have not yielded any observation yet. We therefore selected the maximum entropy approach, implemented in Maxent version 3.4.1 (Phillips et al, 2006, 2017) that is widely used to assess the distribution of a species when only presence data is available. This method discriminates environmental conditions at presence locations against the overall conditions prevailing in the study area (i.e. at background locations) to find the probability distribution that maximizes the entropy while fitting the best possible distribution of the species data.

Each of the ten datasets prepared from the casual observations of immature bearded vultures per season (unfiltered dataset plus the nine filtered datasets, see above) was randomly split into two parts. One part, comprising 70% of the observations, was used for model training, and the remaining part (30%) was used as a testing dataset to evaluate the final model. The training dataset was further split into five random folds to perform cross validation and each model was trained using the same set of 10,000 randomly selected background locations. The whole analysis was conducted in R (R Core Team, 2019) through the RStudio software (RStudio Team, 2018) by using the R package *SDMtune* (see Vignali et al., 2020, for the explanation of the functions used in this analysis). For each dataset, the model was selected according to the following procedure. First, we reduced the initial set of environmental variables by removing highly correlated predictors (Spearman's $|r_s| \geq 0.7$ based on 30,000 random locations) using the function *varSel*. Model hyperparameters were set to default values (i.e. feature classes: linear, quadratic, product and hinge; regularization multiplier: 1, maximum number of iterations: 500). We used the permutation importance to rank variable contributions and the mean training AUC across the five cross validation folds as performance metric. Second, we fine-tuned the models' hyperparameters with the *optimizeModel* function using only the selected variables, checking for the increase in the mean validation AUC across the five cross validation folds. The best set of hyperparameters was searched among the following values: 1) feature classes combinations: lq, lh, lqp, lqh, lph, lqph, with l representing linear, q quadratic, p product and h hinge; 2) regularization multiplier ranging from 0.1 to 2.9 with increments of 0.2; 3) maximum number of iterations: 300, 500 or 700. Third, starting from the model with the tuned hyperparameters combination, we removed variables with a low permutation importance (<2%) by means of the *reduceVar* function, using the Jackknife approach to control for the decrease in the mean validation AUC across the five cross validation folds. Finally, we trained the final, optimized model with all data (i.e. without cross validation).

We evaluated the model's performance by computing the AUC for two testing datasets: the one generated from the same pull of data (i.e. 30% of data held apart), and the one prepared from the GPS locations collected in the same time period (between 2004 and 2014). These two different evaluation datasets were used to select the best filtering approach, and consequently the best model, for the given season. The best season-specific filter was then applied to the corresponding dataset of casual observations of adult bearded vultures and the same method as described above was applied to perform variable and model selection.

Each of the final models was projected to the full extent of the study area by applying the cloglog transformation (Phillips et al., 2017) to the raw output of the model. The four resulting raster maps, representing the predicted probability of species occurrence, were aggregated by selecting the maximum value of the four overlapping pixels. This way we summarized the results to a final unique map that accounts for the requirements of both age classes during both seasons. Probability maps were converted into presence/absence maps using the threshold value that maximized the sum of sensitivity (i.e. proportion of presence locations correctly predicted) and specificity (i.e. proportion of absence locations correctly predicted) on the training dataset. This threshold has been suggested as a good criteria to convert continuous probabilities into a binary map when only presence data are available (Liu et al., 2013). As a final step, we created a map of potential bearded vulture − wind turbine conflicts (hereafter referred to as potential conflict map) by summing the values of the four presence/absence maps. This map has pixel values ranging from zero to four, with zero indicating areas not suitable for the species (i.e. predicted as absence in each of the four models), and four suitable areas for both age classes during both seasons, and therefore areas particularly sensitive with regard to potential threats to the species.

## 3. Results

### 3.1. Species data

A total of 2364 casual observations were retained in the unfiltered datasets, with 630 and 474 observations of immatures during the warm and cold season, respectively, and 719 and 541 observations of adults during the two seasons, respectively (Fig. 1). The number of locations sampled from the GPS fixes varied depending on the number of tagged birds (44 used in the analysis) available for the respective time frame, season and age class (Table 2). On average, a GPS device was active for 25 months with a range of 4−69 months.

### 3.2. Filtering

Applying a filter to the casual observations generally improved the predictions on the independent datasets generated from the GPS locations, for both seasons (Fig. 2). However, the environmental filter built using the distance from roads and the distance from cableways/ski-lifts outperformed the other tested filters. Accounting for the highest testing AUC values on the GPS dataset, we selected the environmental filter created with 80 equal bins (e80 in Fig. 2) for the cold season. For the warm season, the environmental filters with 100 and 200 equal bins had a similar effect. We decided for the one with 200 equal bins (e200 in Fig. 2) given that it holds a narrowed difference between training and testing AUC. Contrasting the bias-corrected predictions against those generated with the unfiltered datasets indicates an over-prediction of vulture occurrence by the latter in most of the study area, especially in the better accessible places (Fig. 3a−b). This effect was less substantial during the warm season (occurring in 58% of the total area) compared to the cold season (in 81% of the total area). Regarding binary predictions of presence and absence (Fig. 3c−d), the application of the filter had an opposite effect for the two seasons. During the warm season the major effect was a reduction of the area predicted as presence (6.9% of the area predicted as presence by the model trained with the unfiltered dataset converted to absence, and 3.9% from absence converted to presence). In contrast, during the cold season, the major effect was an increase of the area predicted as presence (2.1% of the area predicted as presence converted to absence, and 8.1% from absence converted to presence).

### 3.3. Models' predictions

All four models performed well with regard to both training ($\geq$0.861) and testing ($\geq$0.830) AUC, underlining their high accuracy in predicting the occurrence probability of bearded vultures independently of age class or season. Yet, compared to the adult birds, the occurrence of immature bearded vultures was slightly less well predicted. When considering the AUC for the GPS datasets collected during 2015−2019, models for the warm season performed better than the models for the cold season (Table 3). The ten breeding sites that were known until 2014 all fall inside the projected potential conflict area. After 2014, twelve new breeding sites were settled as a result of range expansion and all but one were correctly predicted. According to the potential conflict map, about 40% of the Swiss Alps (10,244 km$^2$ ranging from 224 to 4420 m a.s.l.) offers suitable habitat for the bearded vulture. In general, the area was larger for immature birds (7097 km$^2$ and 5362 km$^2$ in the warm and cold season, respectively) than for the adults (6060 km$^2$ and 5421 km$^2$ in the warm and cold season, respectively).

### 3.4. Ecological requirements

The environmental variables that contributed most (permutation importance) to explaining bearded vulture's habitat in the warm season were the probability of ibex occurrence, gneiss frequency and the frequency of geological substrates other than granite, limestone, and gneiss (42.7%, 20.3%, and 9.3% for immature birds, and 34.2%, 15.9%, and 9.5% for adult birds, respectively, Fig. 5a). Vulture occurrence increased with an increasing availability of ibex, whereas gneiss and other rock types were avoided in favor of limestone substrate (Fig. S1-2). During the cold season, the most important environmental variables driving the habitat selection differed for the two age classes. Whereas immature bearded vultures selected areas with a high probability of Chamois occurrence (22%), an intermediate solar radiation (12%) and a low forest frequency (8.5%) (Fig. 5b), low

**Table 2**
Sample size of the bearded vulture GPS locations used in the analysis. Each dataset was randomly sub-sampled from the total amount of GPS fixes collected within the study area, retaining two locations per month after excluding the first eight weeks of recordings due to proximity to release site during the first weeks following fledging. Locations were sampled separately per age class, season, and time periods (in parenthesis the number of tagged birds from which the sample has been extracted).

| Age class | Season | 2004−2014 | 2015−2019 |
|---|---|---|---|
| Immature | Warm | 237 (N = 20) | 363 (N = 25) |
| Adult | | NA | 178 (N = 10) |
| Immature | Cold | 203 (N = 18) | 281 (N = 23) |
| Adult | | NA | 154 (N = 10) |
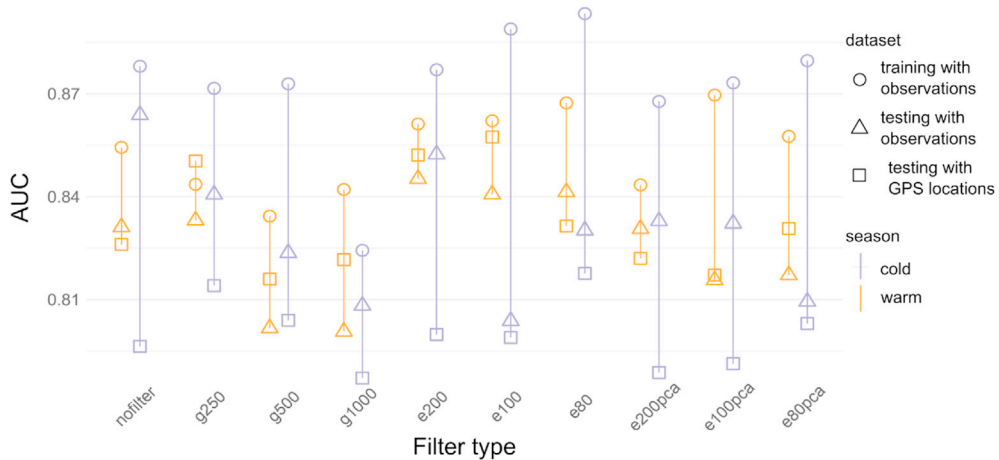
**Fig. 2.** Evaluation of the models trained with the datasets generated by applying the different filtering methods and intensities (the prefixes g and e refer to geographical and environmental filters, respectively, see Material and Methods for details) to the casual observations of immature bearded vultures during the warm (May−October, in orange) and cold (November−February, in violet) season, respectively, provided as the area under the receiver operating characteristics curve AUC. Circles represent the AUC values for the training datasets, triangles for the testing datasets held apart from the casual observations, and squares for the independent GPS locations collected in 2004−2014. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)
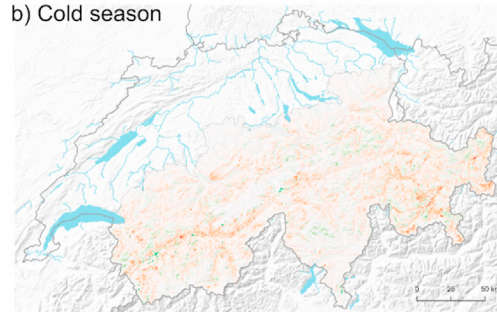


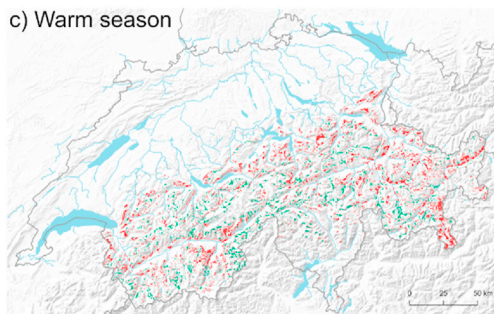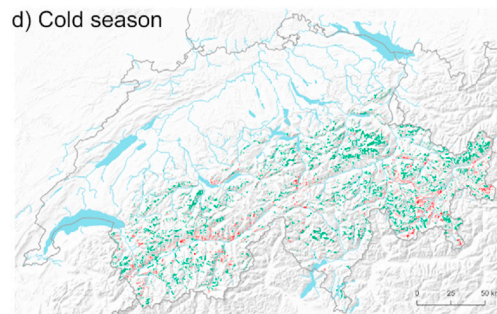**Fig. 3.** Error maps showing the difference between the model results based on the filtered and the unfiltered datasets, with positive and negative values showing where filtering increased or decreased the predicted occurrence probability of immature bearded vultures, respectively, during the warm (a, May−October) and cold (b, November−April) season. Increases in probability, due to the use of the filter, are displayed as a green gradient, while decreases are displayed as a red gradient. The last two maps show the changes occurring in the derived presence/absence maps (see Material and Methods for more detail) for the warm (c) and cold (d) season. The presence/absence map produced with the unfiltered dataset was subtracted from the one produced with the filtered dataset. Changes from suitable to unsuitable are colored in red, while changes from unsuitable to suitable are colored in green. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

**Table 3**

Model performance measured as the area under the receiving operating characteristic (ROC) curve (AUC) (Fielding and Bell, 1997) of the four models predicting habitat suitability for immature and adult bearded vultures in the warm and cold season, respectively. The AUC is provided for the training (Training AUC) and testing (Testing AUC) datasets, and for the testing dataset sampled from the GPS locations (Testing AUC GPS) collected during 2015−2019 (in parenthesis the number of observations included in each dataset).

| Age class | Season | Training AUC | Testing AUC | Testing AUC GPS |
| --- | --- | --- | --- | --- |
| Immature | Warm | 0.861 (N = 417) | 0.845 (N = 179) | 0.809 (N = 363) |
| Adult | | 0.909 (N = 474) | 0.879 (N = 203) | 0.818 (N = 178) |
| Immature | Cold | 0.893 (N = 276) | 0.830 (N = 118) | 0.759 (N = 281) |
| Adult | | 0.899 (N = 265) | 0.893 (N = 113) | 0.714 (N = 154) |

levels of precipitation (21.5%), intense solar radiation (16.6%), and a high probability of ibex presence (13.4%) were most important for adult birds (Fig. S4).

*3.5. Wind turbines*

Within the study area 15 big to medium size wind turbines (hub height 46−119 m, blade diameter 40−102 m) are present, 10 thereof arranged in three wind farms consisting of 2−4 wind turbines each, and five standing singly (Bundesamt für Energie BFE, 2014). Of those, two single wind turbines and two wind farms are located within the area predicted suitable for the bearded vulture (i.e. potential conflict map with values greater than zero). Furthermore, from the 106 wind turbines planned but not yet erected in the Swiss Alps, 35 are located inside suitable bearded vulture habitat according to our model predictions.

## 4. Discussion

We estimated the potential distribution of the bearded vulture across the Swiss Alpine range, accounting for differences between the prospecting and settling phases, and between the warm and cold seasons. This delivered new insights into the ecological requirements of the species, which allowed delineating areas with a high − contemporary and future − probability of species occurrence, i.e. where conflicts with wind energy development will likely occur. Given that our models were mainly based on simple casual observations, which are today readily available from existing data-collection platforms where private naturalists report their findings, the approach used here would be easily transferable to other contexts. This study also establishes, however, that despite their great value for conservation purposes, casually collected data should not be used without cautiously checking for inherent issues and biases that may otherwise lead to flawed predictions.

*4.1. Filtering*

Reducing or eliminating the spatial biases affecting observational data should be a prerequisite to any species distribution models (SDM). This is because sampling bias has been proven to artificially inflate evaluation metrics (Hijmans, 2012; Veloz, 2009). Although the effect of the filtering techniques varies with their intensity (Castellanos et al., 2019; Varela et al., 2014), data are often filtered using a predefined filter size, without exploring the effect of its gradient intensity on the specific dataset (Galante et al., 2018; Liu et al., 2019; Rose et al., 2020; Santangeli et al., 2019). In our study, we tested different procedures and intensities and introduced a new alternative option by restrictively applying the environmental filter to the two variables that define site-accessibility (road and cableways/ski-lift network). This turned out to provide the best performing filter type in terms of model performance on the independent dataset. The dataset sampled from the GPS locations collected during 2015−2019 allowed us to further estimate the model's ability to predict a future population expansion into areas that had apparently not been occupied previously. This is crucial for the bearded vulture since its Alpine population has not yet reached carrying capacity while the objective of the whole modelling exercise was to delineate sensitive areas from the viewpoint of wind industry development.

*4.2. Ecological requirements*

The ecological requirements of bearded vultures vary according to both age class and season. While the requirements of immature and adult birds were quite similar during the warm season (comparable permutation importance of the three top ranked environmental variables and similar response curves), clear differences emerged between seasons and between age classes within the cold season. Food availability and geological substrate mainly determined the distribution during the warm season. Whereas the species avoids areas characterized by gneiss and rocks of "other substrate types" (i.e. other than limestone, granite and gneiss) (Fig. 5 and S1-2), areas dominated by limestone were positively selected (Fig. S1-2). This is additionally supported by the high percent contribution of this variable (Fig. S5) which ranks second for adults and third for immatures, corroborating former findings (Hirzel et al., 2004). Indeed, limestone regions are characterized by fine-grained screes that offer the best conditions for bone-breaking, a key feeding strategy of bearded vultures (Hirzel et al., 2004).

During the cold season food availability was again among the most important environmental variables, but with a noticeable difference between immature and adult birds. For immature bearded vultures, chamois presence was most important, while for adult birds ibex presence was ranked as the third most important variable. This shift of food availability from the first to the third rank suggests that the habitat selection of adults in the cold season may be driven more by climatic conditions than food supply. Average precipitation and solar radiation were indeed the environmental variables with the highest permutation importance, with a negative and positive response type, respectively. Conceivably, this may be because adult birds could be constrained by the availability of favorable winter conditions in nest surroundings. In effect, the breeding season in this species starts in the middle of the winter, with egg laying between December and February, i.e. when environmental conditions are particularly harsh, with a probable preference for warm and dry breeding cliffs.

The few discrepancies between this study and that by Hirzel et al. (2004) are, first, that chamois did not play a key role in the latter, contrary to ibex. This is maybe due to the fact that Hirzel's et al. investigations were carried out in the southwestern Swiss Alps were chamois is uniformly widespread, while there is high spatial variability in chamois occurrence when considering the entire Swiss Alpine range. Second, limestone frequency was the most important variable for both immature and adult birds in that previous model. If we also evidenced a key role of limestone, this condition was less important than food availability during the warm season or climatic conditions during the cold season. This discrepancy could again be explained by both a greater extension of our study area and because we distinguished between seasonal requirements. Alternatively, our observational dataset was more recent, which may less well reflect species' key ecological preferences given that bearded vultures have meanwhile started to colonize less optimal areas due to population growth and hence expansion. Sheep and goat densities, as an alternative food source, were discarded during the variable selection process. This was not a real surprise because domestic ungulates provide exploitable carcasses almost exclusively during the warm season: in winter they are in stables.

### 4.3. Distribution maps and wind energy development

The differences in habitat selection between the two age classes and seasons translated into distribution maps that somehow spatially differ in terms of habitat suitability. Specifically, if highly suitable areas fairly widely overlap between seasons and age classes (Fig. 4a−d), the synthetic map obtained by taking the maximum pixel value from each of the four maps (Fig. 4e) embraces the whole complexity of situations and provides basic information for conservation management. Furthermore, the potential conflict map (Fig. 4f) ranks suitable areas into four classes and provides a readily useable tool for landscape planning and environmental impact assessments. This map indeed can be considered as a spatial-explicit estimation of the "sensitivity" of a given area from the perspective of bearded vulture conservation. In effect, it highlights sensitive areas that may easily be overlooked otherwise, in particular if bearded vultures are not yet regularly spotted there, i.e. it informs whether planning a wind turbine in a given area is a sensible option from the viewpoint of wildlife protection. However, this does not mean that outside these sensitive areas (i.e. in areas tagged with zero probability of risk) collisions with wind turbines can entirely be excluded, and that impact assessments would not be required. It simply means that the likelihood of a wind turbine-project to be opposed because of conflicts with bearded vulture conservation would be much lower there than in the other, more sensitive zones (1−4).

The Swiss Wind energy concept, which delineates areas suitable for wind energy production, had proposed exclusion zones within a 5 km radius around all bearded vulture nesting sites known at the time (N = 10; 2014), aiming to reduce *a priori* the risk of collisions of bearded vultures with turbine blades in future installations (Bundesamt für Raumentwicklung ARE, 2017). Yet, the rapid expansion of the population has led to 22 breeding pairs in 2019 in Switzerland. Although not yet considered by the wind energy concept, all these novel sites are correctly predicted by our spatial models (only one nest location is situated 50 m beyond an area predicted as suitable for the species). It should be noticed that we obtained a correct prediction of the novel nesting sites even if our models have been trained using only observations spanning from 2004 to 2014 (the last being the reference year in the wind concept). This demonstrates the power of predictive models to project and anticipate conflict zones, paving the way for more accurate estimates of critical sites for wind energy development. Further support for such models is provided by the fact that the breeding site of nine "pairs" have changed over time, with relocation distances ranging from 280 to 3632 m (median 1081 m), with all but one of these new sites (40 eyries for 22 territories) falling within the areas delineated by the potential conflict map. For all these reasons, a simple delineation of buffer areas around known bearded vulture nest sites is not a meaningful way to guarantee the protection of a reestablishing breeding population.

A recent Europe-wide study ranked Switzerland among the countries with the lowest *per capita* wind energy production (Iten and Nipkow, 2019), but the Swiss government has planned to boost, i.e. subsidize this industry with the objective to reach a yearly energy output of 4,3 TWh by 2050 (Bundesamt für Raumentwicklung ARE, 2017). Areas with constant and sufficient wind speed in terms of economical profitability are rare, and mostly located in the Jura mountains and in the ridges and passes of the Alps − the latter being within the potential range of the bearded vulture. Numerous new wind turbine projects are thus expected in the coming years, with already 106 new planned wind turbines within the Swiss Alps, and several additional projects being currently evaluated. Many of these new plants (N = 71) are outside of our potential conflict map but sometimes not far from the areas predicted as suitable for bearded vulture (minimum distance 7 m, maximum distance 17,557 m, median value 649 m). This calls for much better, i.e. evidence-based land-planning strategies. In this context, the present model represents a real asset.
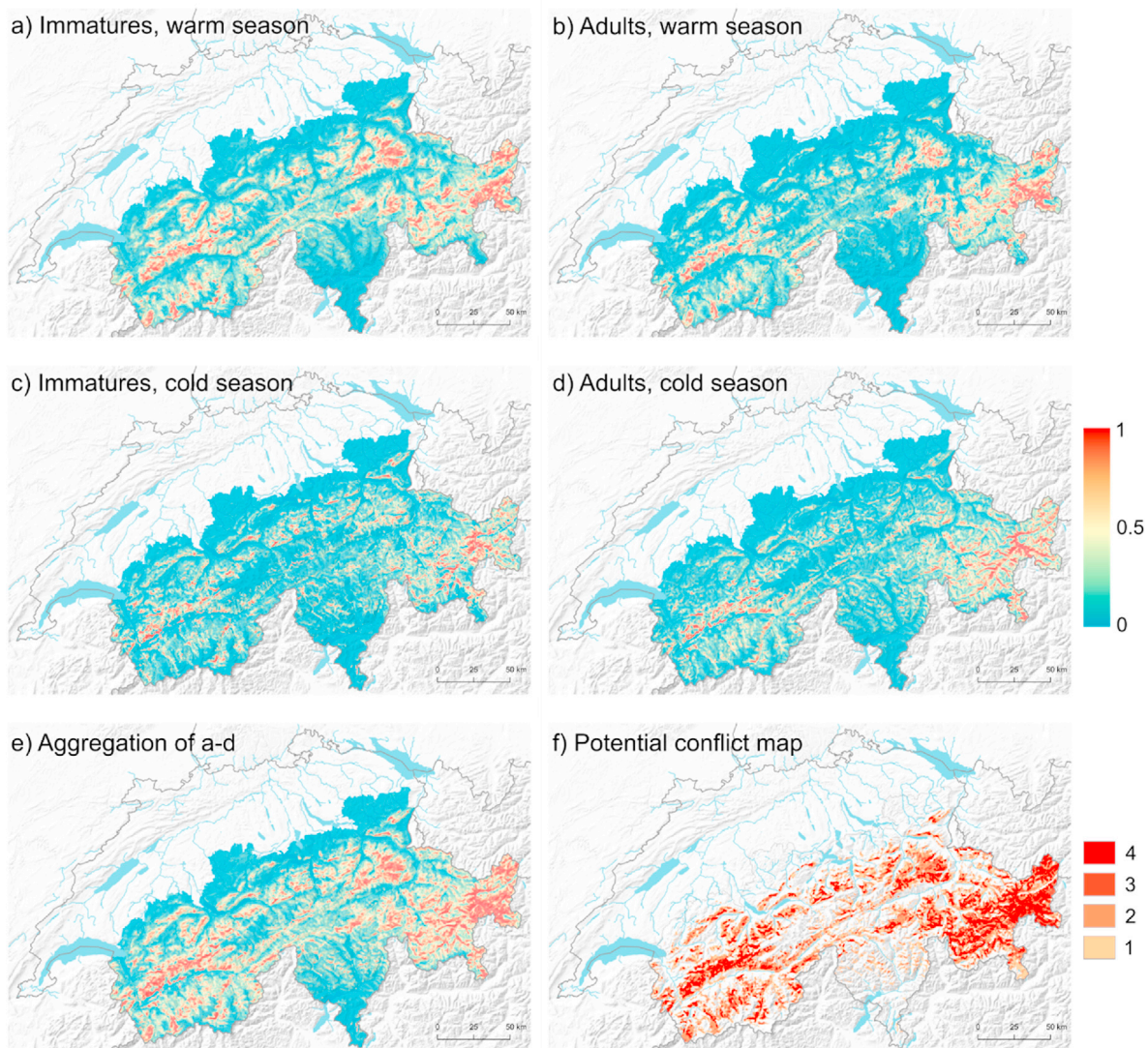
**Fig. 4.** Predicted probability (gradient from blue, zero probability to red, high probability) of bearded vulture occurrence, projected to the entire study area for immatures during the warm (a) and cold (c) season, and for adults during the warm (b) and cold (d) season, respectively. The map e results from the aggregation of the four raster maps a-d, taking the maximum value out of the four overlapping pixels and f is the potential conflict map (see Material and Methods for more detail); the red scale in f indicates the number of models out of four that predict that area as suitable. The map f can thus be considered as a spatial-explicit estimation of the "sensitivity" of a given area from the perspective of bearded vulture conservation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

### 4.4. Potentials and limitations

Our potential conflict map delineates areas that are suitable for the species, incorporating requirements of all life stages throughout the year cycle. Accounting for age-related habitat selection patterns is crucial for a species like the bearded vulture that explores vast areas during its teenage and becomes more and more territorial when becoming sexually mature (Margalida et al., 2016). Season-related requirements are not less important given that winters in mountain environments can be harsh, limiting the availability of suitable nesting sites and food resources. The potential conflict map delineates suitable areas in a conservative way, meaning that even if an area is predicted suitable for the species, it may not necessarily represent a zone of conflict with wind energy development. This occurs for instance when bearded vultures overfly some areas only during commuting, i.e. at altitudes far above the air space potentially swept by the rotor blades of wind turbines. On the other hand, a conservative approach avoids overlooking species-relevant areas, thus providing a broad-scale framework that will serve as a base for refined risk assessments of potential collision risks locally.
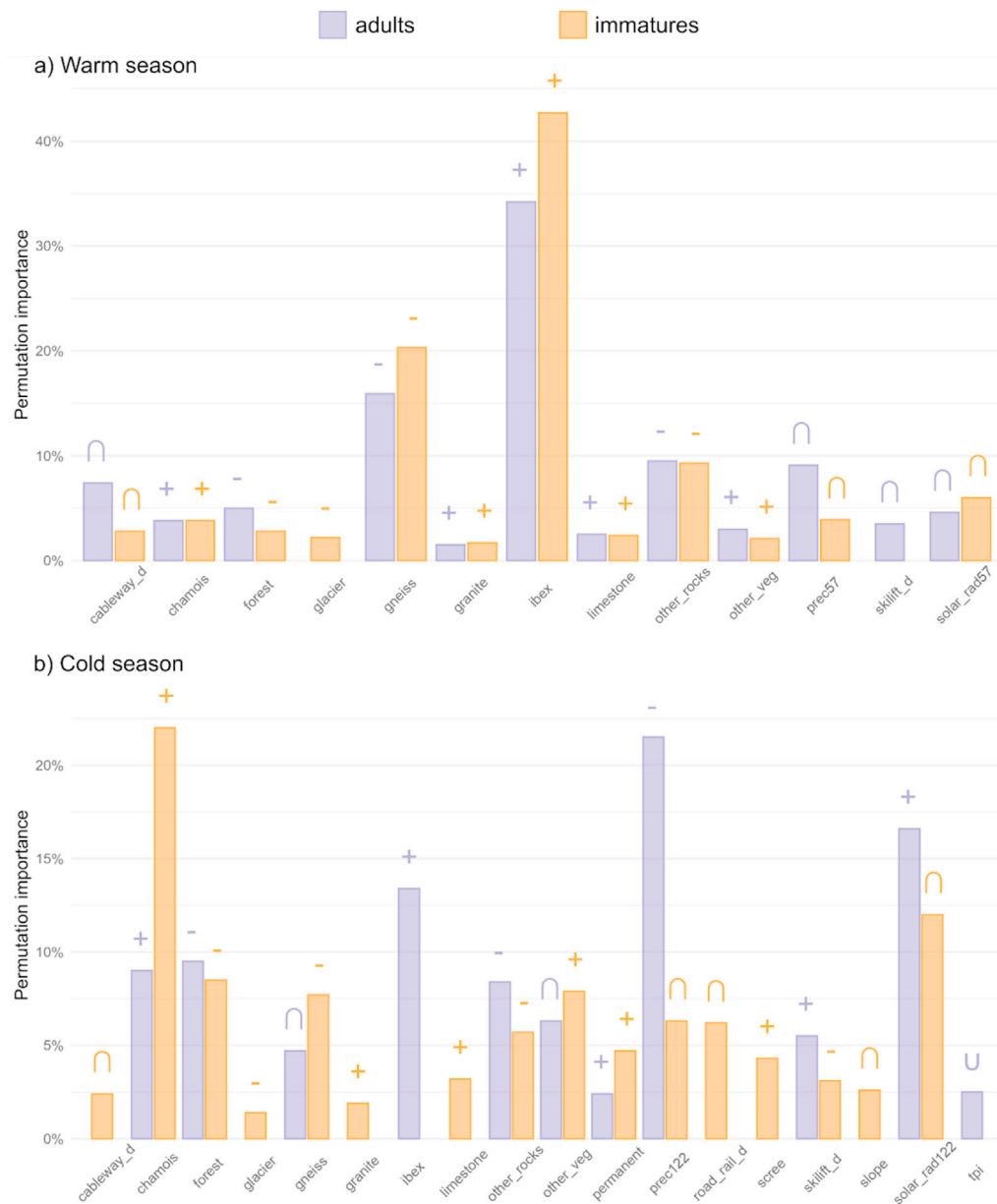
**Fig. 5.** Variable importance, given as permutation importance, of the environmental variables retained in the final models predicting species occurrence in the a) warm and b) cold season of adult (violet) and immature (orange) bearded vultures. The symbol above the bar indicates the response type for the univariate model trained using every variable separately (for the response curves see Figures S1-4), with +, −, ∩ or ∪ indicating a positive, negative, unimodal or bimodal response, respectively. The relative (normalized %) permutation importance is computed by randomly shuffling the values of each environmental predictor at a time for both training and background locations, evaluating the model with the shuffled data, and measuring the drop in training AUC. See Table 1 for the variable abbreviations and descriptions. The variable importance measured as Maxent percent contribution [sensu Phillips (2017)] is provided in Fig. S5. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The single-species approach used here is of course inherently limited. There are other vulnerable species that should also be considered when estimating the collision risks generated by wind turbines, particularly soaring raptors with similar life-history traits and flight behaviour. The golden eagle (*Aquila chrysaetos*), for example, is another large resident raptor present in the Swiss Alps that is potentially at risk given its large home range size and extensive daily movements. In this respect, combined spatial analyses conducted on the potentially most impacted mountain species would deliver a comprehensive spatial overview of the foreseen conflict areas to better inform management.

## 5. Conclusion

Here we demonstrate that, when dealing with reintroduced or spreading species, the use of buffer areas around extant nesting locations for precluding any potential threats — such as the collision risks generated by wind turbines — does not guarantee a protection of all key areas relevant for a breeding population. Our approach allows not only identifying key species' ecological requirements but also predicting its future range expansions into previously unused areas. The resulting habitat suitability maps and the potential conflict map represent a set of predictive spatial projections of future conflicts with wind energy production. The potential conflict map accounts not only for the breeding fraction of the population but also for dispersing and roaming immature individuals, thus considering the whole life cycle for enhancing conservation. We stress that our maps are intended for general guidance purposes but can in no case replace the environmental impact assessments required for planning new wind turbines. We nevertheless hope our maps will help wind energy developers as well as planners of aerial infrastructures such as electric power lines, cable cars and ski-lifts, at an early stage of the planning process, to identify areas where bearded vulture would encounter a high risk of collision, which might compromise a project from the onset.

## Declaration of competing interest

The authors declare that there is no conflict of interest.

## Acknowledgments

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01405.

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