Distribution, status, and recent population dynamics of Alpine ibex Capra ibex in Europe

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Abstract: Despite its recent successful and well-documented reintroduction history, a comprehensive and current update of the distribution and status of the Alpine ibex Capra ibex is lacking. As some concerns persist about its conservation, a status update appears essential for future conservation and management strategies on a large scale. We provide an exhaustive update of the geographic range of the species, alongside estimates of its current abundance and population trends from 2004 to 2015. We gathered census and distribution data for all the Alpine ibex colonies from management authorities and research groups that monitor them in different countries, and from the literature and publicly available reports. We produced a distribution map, reported the number of individuals observed in the most recent censuses, and estimated global, national, and local population trends using Bayesian hierarchical models. Our model estimated that there were a total of 55297 Alpine ibex in the Alps in 2015 (lower 95% credible interval [CrI]: 51157; upper 95% CrI: 62710). The total number of individuals appears to have increased slightly over the last 10 years from the 47000-51000 estimated in previous reports. Positive population trends were observed in Switzerland and Italy, while no trend was apparent in France. For Austria, Germany, and Slovenia, there were insufficient data to estimate a trend. The slopes of the colonies' trends were positively correlated with the year of colony foundation. The geographic range of the Alpine ibex does not seem to have increased in size in recent years, although the accuracy of the spatial data varies among countries. The periodic and standardised collection of census data for all colonies and a common policy of data sharing at a European level appear essential for monitoring the global trend of this species and for planning balanced conservation and management actions.

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REVIEW

Distribution, status and recent population dynamics of Alpine ibex *Capra ibex* in Europe

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ABSTRACT

1. Despite its recent successful and well-documented reintroduction history, a comprehensive and

current update of the distribution and status of the Alpine ibex *Capra ibex* is lacking. As some concerns persist about its conservation, a status update appears essential for future conservation and management strategies on a large scale.

2. We provide an exhaustive update of the geographic range of the species, alongside estimates of its current abundance and population trends from 2004 to 2015.

3. We gathered census and distribution data for all the Alpine ibex colonies from management authorities and research groups that monitor them in different countries, and from the literature and publicly available reports. We produced a distribution map, reported the number of individuals observed in the most recent censuses, and estimated global, national, and local population trends using Bayesian hierarchical models.

4. Our model estimated that there were a total of 55297 Alpine ibex in the Alps in 2015 (lower 95% Credible Interval [CrI]: 51157; upper 95% CrI: 62710). The total number of individuals appears to have increased slightly over the last 10 years from the 47000-51000 estimated in previous reports. Positive population trends were observed in Switzerland and Italy, while no trend was apparent in France. For Austria, Germany, and Slovenia, there were insufficient data to estimate a trend. The slopes of the colonies' trends were positively correlated with the year of colony foundation.

5. The geographic range of the Alpine ibex does not seem to have increased in size in recent years, although the accuracy of the spatial data varies among countries.

6. The periodic and standardised collection of census data for all colonies and a common policy of data-sharing at a European level appear essential for monitoring the global trend of this species and for planning balanced conservation and management actions.

INTRODUCTION

The Alpine ibex *Capra ibex* is a charismatic mountain ungulate endemic to the European Alps, where it occurs in all Alpine countries (France, Italy, Switzerland, Lichtenstein, Austria, Germany, Slovenia). Although its elevational range goes from 750 m above sea level (asl) in the Vercors

Regional National Park, France, up to more than 3000 m asl in the Western Alps, most Alpine ibex populations are found between 1500 and 3000 m asl, and the most suitable habitat for this species consists of the alpine meadows and rocky cliffs found at this elevation (Grignolio et al. 2003, 2007). The current distribution is, however, a consequence of the recent history of the species which, after suffering almost total extinction in the 19th century, survived only in a restricted area in the north-western Italian Alps and was the object of extensive reintroductions throughout the whole Alpine arc in the 20th century (Stüwe & Nievergelt 1991).

The origin of Alpine ibex as a species is still debated (Manceau et al. 1999, Pidancier et al. 2006, Kazanskaya et al. 2007), but the ancestors of Alpine ibex are likely to have migrated to Europe from Central Asia around 300000 years ago (Cregut-Bonnoure 1992). At that time, the species occupied its largest range, also outside the Alpine region. At the end of the Riss Glaciation, as a result of reforestation of low-elevation areas, the Alpine ibex became restricted to the Alpine region. In the Middle Ages, the Alpine ibex was still spread throughout the Alps, but intensive hunting, following the development of firearms, brought most populations to extinction (Grodinsky & Stüwe 1987). The first signs of the decline of the species are dated to the late Middle Ages and, in the following centuries (16th – 18th), Alpine ibex gradually disappeared from all Alpine countries except Italy. In Austria and Slovenia, Alpine ibex began disappearing from the beginning of the 18th century. In Switzerland and France, the decline was more progressive, but the last signs of Alpine ibex presence were at the beginning of the 19th century in the Wallis canton. At the beginning of the 19th century, there were no more than a hundred individuals left in a restricted area surrounding the Gran Paradiso Massif, Italy (Grodinsky & Stüwe 1987). Hunting was then prohibited by a Royal decree in 1821 and, thanks to active protection of the species and the institution of the Gran Paradiso Royal Hunting Reserve by King Vittorio Emanuele II in 1856, the population increased to approximately 3000 individuals at the beginning of the 20th century. In the first half of the 20th century, around 90 ibex were captured in the Gran Paradiso area and brought into captive-breeding programs at two Swiss wildlife parks, St. Gallen and Interlaken (Stüwe & Scribner 1989). In the last century, the species was reintroduced first in Switzerland and then in all the other countries of the Alps (Tosi et al. 1986, Wiersema 1990, Giacometti 1991, Stüwe & Nievergelt 1991). Reintroductions were performed from 1911 to 2014, with most of the colonies (82%) founded between 1950 and 2000. 12% of the colonies were founded before 1950, mostly in Switzerland and Italy (Giacometti 1991) plus two in France and one in Germany, and only 6% were founded after 2000. Today, the species is present on the entire Alpine arc, although its range is still fragmented and there are some suitable areas that are not yet occupied (Gruppo Stambecco Europa, Alpine ibex European Specialist Group [GSE-AIESG] unpublished data).

The Alpine ibex is included in the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, Appendix III – Protected Fauna Species, 1979) and in the European Directive 43/92/CEE "Habitat", Annex V (Updated with Directive 97/62/CE, 27 October 1997).

A map of the geographic range of the species is included in the International Union for Conservation of Nature's (IUCN) Red List of threatened species (Aulagnier et al. 2008). The IUCN assessment classifies the Alpine ibex as a species of Least Concern "in view of its wide distribution, presumed large population, and because it is not declining at nearly the rate required to qualify for listing in a threatened category", but also declares that "the species needs conservation action to prevent future decline" (Aulagnier et al. 2008). Indeed, in the last few years, several concerns have arisen about the conservation status of the species. The strong bottleneck that occurred in the 19th century dramatically decreased the genetic variability of the species. The average heterozygosity of Alpine ibex is one of the lowest registered in wild mammals (Biebach & Keller 2010), and the presence of inbreeding depression has been shown in the Gran Paradiso colony, the only remnant (not reintroduced) Alpine ibex population in the Alps (Brambilla et al. 2015). Furthermore, inbreeding reduced the intrinsic per-capita population growth rate in Alpine ibex colonies (Bozzuto et al. 2019). Alpine ibex can interbreed with domestic goats *Capra hircus*, and genetic analyses of the major histocompatibility complex region revealed that successful hybridisation events between the two species, with consequent introgression, have occurred in the past (Grossen et al. 2014). Moreover, despite the general recovery of Alpine ibex in the recent decades on a global scale, the remnant Gran Paradiso colony has shown strong declines (Jacobson et al. 2004, Mignatti et al. 2012). Furthermore, trends in the abundance of the species in different countries reported during the GSE-AIESG meetings in 2012 and 2015 indicate that its status and population dynamics are not consistent throughout the Alps. Finally, direct and indirect consequences of epidemic diseases have affected several recently reintroduced colonies, as well as established ones. Examples are sarcoptic mange in the eastern Alps (Carmignola et al. 2006), brucellosis in the Bargy Massif, France (Mick et al. 2014), respiratory diseases in the Vanoise National Park, France (Garnier et al. 2016), and infectious kerato-conjunctivitis in several areas, including the Gran Paradiso where infectious kerato-conjunctivitis was found to be related to low genetic variation at the major histocompatibility complex region (Brambilla et al. 2018).

The rescue and restoration of Alpine ibex represents one of the most successful conservation efforts in Europe. The reintroduction history is well documented, and information on population size is available for all the reintroduced colonies, as most of them were monitored, although with varying effort, at least in the first years after the releases. However, the different management strategies in the European countries (for a brief description of the management regulations in the European countries hosting Alpine ibex populations, see Appendix S1) and the lack of a communal policy on data sharing have resulted in fragmented information about the current status of the species. Some information is published in regional and national reports (also reviewed by De Danieli & Sarasa 2015), but much remains unpublished. Despite its recent successful reintroduction history and the strong interest in this charismatic species, a comprehensive and current update of the distribution and status of Alpine ibex is still lacking. Considering the concerns about the conservation of the species, such an update appears to be timely and essential for planning future conservation and management strategies on a continental scale.

We provide an exhaustive update of the current geographical range, as well as estimates of abundance and local and global population trends, of the Alpine ibex in the Alps from 2004 to 2015.

METHODS

Definition of distinct populations and census method

For this project, we use a working definition of the term 'colony' to describe the distribution of populations of Alpine ibex. When possible, we considered the different reintroduced nuclei, which are historically known and are under different management authorities, as distinct. However, this was possible only for some areas where the colonies are isolated, and there is a clear spatial separation among them. For this reason, we considered differently 1) areas where the oldest and largest colonies are located; 2) areas where the distribution of the animals is continuous and difficult to separate into distinct nuclei; and 3) trans-boundary colonies. For 2) and 3), we defined the colonies following administrative boundaries of the different management authorities that perform censuses.

Block counts, also referred to as ground counts, are the most common method used to assess population size in Alpine ibex colonies. The areas occupied by each colony are divided into sectors, and expert observers with good knowledge of the territory count ibex in each sector by means of binoculars or telescopes from footpaths or vantage points. Within an area, the count for all sectors should be conducted in a short time (however, this is not always possible due to observers' availability or environmental constraints). During the surveys, the total number of observed ibex is recorded. In most of the areas, group size, location and age and sex classes are also recorded. As different authorities do not always perform simultaneous censuses, overlaps in counts are possible due to animal movement across administrative boundaries. However, the risk of double counts is low, as neighbouring authorities tend to coordinate the census. Errors in counts due to missing animals may not be negligible, and for this reason, the numbers presented in this study have to be considered as minimum counts (Largo et al. 2008). For a summary of the colonies considered in the study and their locations, see Appendix S2.

Data collection

Data on the abundance and distribution of Alpine ibex were directly requested from management authorities or research groups that monitor colonies in different countries after informing them about the aims of the project. When available, data published in the literature or publicly available online were also gathered. All individuals, public bodies, and research groups that provided data are listed in the Acknowledgements section. A European-wide dataset was built including data from all colonies. When available, the data collected for each colony were: a) the most recent census data; b) number of individuals counted in previous censuses; c) year of colony foundation; d) season of the census; e) information about the area used by ibex during the year (winter and summer range) and any geographical information available; f) sex and age structure composition of the colony. The latter information (d-e-f) was not explicitly used for the analysis of this study, as complete and reliable data were not available for all countries, but was nevertheless stored in the database, which is constantly being updated by the GSE-AIESG with new data and information. The minimum information available for all colonies were: name, country, spatial extent of the occupied area (accuracy differs between colonies), number of individual ibex counted in the last census, and year of the last census. The colony of Gasthofgebirge, Austria, was included in the count data but was not used for models of population dynamics, as its foundation was too recent (2014).

Range map

The current geographic range map for Alpine ibex in the European Alps was created using a Geographic Information System (Q GIS 2.18.0 – Las Palmas, QGIS Development Team 2016): the shapefile containing the area occupied by each colony and the associated census data were uploaded to a project containing a digital terrain model of the Alps (reference system WGS 84, UTM 32 N). The area occupied by each colony was defined based on the information received from the management authorities or research groups that monitor colonies (see point e in the previous paragraph). This information was shared as digital shapefiles or as scanned paper maps. In the latter case, the maps were sufficiently accurate to allow us to import them into the QGIS environment, reference them (using the Georeferencer GDAL plugin), and manually digitise them. All the polygons were finally merged into a single shapefile. The density of ibex in each of the different colonies was calculated as the total number of animals counted divided by the area occupied by each colony. In order to increase the accuracy of the area occupied by each colony, we removed unsuitable habitat categories. In order to do this, we intersected the layer of the ibex colonies with the layer of the Corine Land Cover (EEA, 2018) and removed from the colonies layer surfaces belonging to the following categories: "Glaciers and perpetual snow", "Road and rail networks and associated land", "Water bodies", "Urban fabric". However, as the accuracy of the area considered to be occupied by each colony varies greatly among them, spatial data were not used for further analyses.

Count data

In order to obtain the current size of the total Alpine ibex population in Europe and to compare it with estimates obtained from the models, we summed the number of individuals of each colony counted in the last census. We counted the total number of individuals in the Alps and the total for each country. To reduce the risk of double counts or of missing animals due to animal movement across administrative boundaries, when possible, we used censuses performed in the same season (winter or summer counts) for geographically close colonies, as most ibex movements occur seasonally.

General model of population dynamics

To model the dynamics of the different colonies, we used a Bayesian hierarchical Poisson model with the year as a fixed effect and the colony (id) and the country as random factors, allowing slopes to vary in each colony. We modelled both random and the fixed effects with a thin-plate spline regression line (k=10) allowing for varying variances (Wood 2003). The model was fitted using the MCMCglmm package (Hadfield 2010) in R v.3.3.3 (R core Team 2016). The model was run for 130000 iterations with 30000 burn-in and a thinning of 100. We did not include any environmental covariates, as the scope of this analysis was purely to describe the dynamics of the different colonies (and thus of the whole Alpine ibex population), rather than to infer the relative importance of environmental variability in predicting trends.

The timespan of the models ranged from 2004 to 2016. However, since several data points were missing for 2016, we chose 2015 as the most recent year with reliable estimations (see Fig. 2), and we present estimates related to 2015 in the Results section. We extracted specific estimates for 177 colonies in the Alps (all the nuclei that are present on the map except Gasthofgebirge, Austria) using the *predict* function in MCMCglmm (Hadfield 2010), not marginalising over the random effects to get colony-specific estimates (marginal = NULL). We obtained predictions and lower and upper 95% Credible Intervals (CrI) on the original data scale (counts) using type="response" in the *predict* function. To estimate the total population size per year, we summed up the posterior mcmc samples for each colony and extracted CrIs after back-transforming to the data scale.

Countries estimates and effects of the year of foundation on modelled population growth

To evaluate population trends for Alpine ibex in each country, we obtained the slope and confidence intervals (CI) for each country from a linear regression model performed on the yearly estimates extracted from the general Bayesian hierarchical model described in the previous section, with the year as an independent variable. As count data for many of the colonies in Austria, Germany and Slovenia were only available for a few years, the trends were modelled only for Italy, Switzerland and France.

The same procedure was used to obtain the population growth rate for each colony (extracting slope and CI from the general model). As more rapid growth is expected in colonies that derive from recent introductions in unoccupied habitats, we tested the effect of the year of colony foundation on population growth rate. This was achieved by modelling individual colony slopes as a function of foundation year with a linear mixed-effects model (lme4 package, Bates et al. 2015), with the country as a random term.

RESULTS

Range map

A geographic range map showing the current distribution of the Alpine ibex colonies is presented in Fig. 1. From a visual inspection of the map, particularly observing the detail of the borders of the area occupied by each colony, it is possible to assess that the spatial resolution greatly varies among colonies and among countries.

An interactive map with the density of Alpine ibex in each colony as well as a graphical representation of the number of ibex counted in each of them from 2004 to 2015 is presented in Appendix S2.

Count data and models of population dynamics

Based on the information gathered from the management authorities or research groups that monitor Alpine ibex, a total of 178 Alpine ibex colonies were identified over the entire Alpine arc. Alpine ibex colonies are present in all the six major Alpine countries: France, Italy, Switzerland, Germany, Austria, and Slovenia plus Liechtenstein with large differences in the number of individuals and colonies for each country. A total of 55297 Alpine ibex (lower 95% CrI: 51157; upper 95% CrI: 62710) was estimated for 2015 by our Bayesian hierarchical model. Summing up all the individuals from the last censuses conducted in all colonies, we obtained a total count of 53154 individuals which falls within the 95% CrIs of our model. Despite an apparent slight increase of the number of individuals, the slope and CI of the linear regression fitted on the estimated yearly counts do not provide evidence of an increasing trend in the whole Alpine ibex population of the Alps in the years covered by this study (2004-2015, $\beta = 662.8$; lower 95% CI: -232.1; upper 95% CI: 1607.0). Count data and model estimates describing the current status of the species in each country (from west to east) are summarised in Table 1.

The recent trend of the species as a whole and in Italy, France and Switzerland, obtained by the Bayesian hierarchical Poisson model are presented below. Graphics representing the number of ibex estimated by the model are reported in Fig. 2 and 3(a-f).

FRANCE

In France, there are 30 Alpine ibex colonies, with a total number of 9002 individuals counted (the last census of different colonies ranged from 2008 to 2016). Few counts were available in recent years, and consequently, CrIs for the yearly estimates for the French colonies are relatively wide (Bayesian model median estimate for 2015: 7775 individuals; lower 95% CrI: 5955; upper 95% CrI: 12286). Despite Alpine ibex abundance in France appearing to show a declining trend over the last 10 years (Fig. 3a), the slope of the linear model does not provide evidence of a decline, since the CIs around the estimate broadly overlap zero (β = -118.8; lower 95% CI: -386.9; upper 95% CI: 404.1).

SWITZERLAND

In Switzerland, there are 45 Alpine ibex colonies, with a total of 17875 individuals counted in 2016. Model estimates indicate 17664 individuals in 2015 (lower 95% CrI: 17398; upper 95% CrI: 17923). Overall, the abundance of Alpine ibex in Switzerland (Fig. 3b) shows an increasing trend over the last decade (β = 306.1; lower 95% CI: 269.7; upper 95% CI: 347.9).

ITALY

In Italy, there are 67 Alpine ibex colonies, with a total of 16471 individuals counted in the years 2012-2017. The Bayesian model estimates 19872 individuals in 2015 (lower 95% CrI: 16847; upper 95% CrI: 25373). The total number of Alpine ibex in Italy (Fig. 3c) seems to show an increasing trend in the last 10 years (β = 464.6; lower 95% CI: 107.8; upper 95% CI: 1,194.0). However, although they do not overlap zero, CIs around the estimated slope for the trend are rather wide.

AUSTRIA

In Austria, 9013 Alpine ibex assigned to 27 colonies were counted in 2015. The boundaries of the areas occupied by the colonies do not seem to be very accurately known (except for the Hohe Tauern colony), possibly because Alpine ibex counts are done by different authorities that do not always collect spatial information. Moreover, different parts of the area occupied by some colonies might be under the authority of different hunting districts, so it is difficult to obtain a precise number of colonies. Count data are not available for each year in each colony, and therefore CrIs around model estimates are relatively wide (model estimates for 2015: 8813; lower 95% CrI: 8491; upper 95% CrI: 9186).

GERMANY

In Germany, 516 individual Alpine ibex assigned to five colonies were counted in the years 2014-2017. The model estimates 549 individuals in 2015 (lower 95% CrI: 327; upper 95% CrI: 1003). The figure seems to highlight a declining trend (Fig. 3e) in the last decade, although it was not possible to draw a firm conclusion about the trend of the species in Germany.

SLOVENIA

The last data from Slovenia, received in 2016, indicated that 277 Alpine ibex have been counted from four colonies in this country (model estimates for 2015: 323; lower 95% CrI: 185; upper 95% CrI: 570). The number of ibex was greatly reduced in the last 10 years due to an epidemic of sarcoptic mange (Iztok Koren, personal communication). However, probably due to the timespan of our models, the declining trend was not evident (Fig. 3f).

Table 1. Number of colonies, and number of individual Alpine ibex *Capra ibex* counted (N counted) and estimated (N estimated) in the European countries in the Alpine Arc. “N counted” was obtained by summing the number of individuals counted during the last census conducted in each population. “Year of last counts” specifies the years in which the last census was conducted. As not all the populations in the same country are surveyed every year, for the same country there may be different

"Year of last counts". "N estimated" represents the number of individuals estimated from a hierarchical Poisson model for the year 2015. "U95CrI" and "L95CrI" are the upper and lower 95% Credible Intervals of the Poisson model for 2015. For Austria, the number of colonies was obtained from the sum of different counting units. "Trend" indicates whether the slopes and CIs provided evidence of positive trends (+) or no trends (=); NA indicates the countries for which it was not possible to model the trend because of insufficient data.

Country	**N colonies**	**Year of last counts**	**N counted**	**N estimated**	**L95CrI**	**U95CrI**	**Trend**
France	30	2008-2016	9002	7775	5955	12286	=
Switzerland	45	2016	17875	17664	17398	17923	+
Italy	67	2012-2017	16471	19872	16847	25373	+
Austria	27	2016-2018	9013	8813	8491	9186	NA
Germany	5	2014-2017	516	549	327	1003	NA
Slovenia	4	2016	277	323	185	570	NA
Alpine arc	178	2008-2018	53154	55297	51157	62710	=

Effects of the year of colony foundation on population growth

The linear mixed effect model for population trends was performed on the slopes of 142 colonies from three countries (Switzerland N=43; Italy N=65; France N=30). The results of the models indicated that the year of colony foundation was positively related with the growth rate of the colony ($\beta \pm$ SE = 0.087 ± 0.034, 95% CI range: 0.020-0.154, R^2=0.215). The slope of the colonies founded in recent times is steeper than that of older colonies.

DISCUSSION

The European distribution of Alpine ibex presented in this study confirms that the species is currently present on the entire Alpine arc, with 178 colonies and more than 53000 individuals. A previous attempt to estimate the total number of Alpine ibex produced a total number of 50195 ± 1012 individuals in 2013 (De Danieli & Sarasa 2015), which is consistent with the estimate of our model for that year.

Comparing the total number of individuals estimated in our study for 2015 (N= 55297; lower 95% CrI: 51157; upper 95% CrI: 62710) with the minimum number reported for 2005-2007 (Apollonio et al. 2009, N= 47000 individuals), with the unofficial report provided during the GSE-AIESG meeting in 2012 (N= 49000-50000 individuals), and with the estimate by De Danieli and Sarasa (2015) for 2013 (N= 49000-51000 individuals), the overall number of individuals appears to have increased slightly over the last 10 years. Nevertheless, our linear model does not provide clear evidence of a numerical increase in the total number of individuals during the years 2004-2015, due to the high level of uncertainty around the estimates.

Alpine ibex are commonly counted using total block counts, although not all areas were surveyed with the same frequency and number of observers. Moreover, most of the colonies were counted in the pre-reproductive spring season, while others were surveyed after the birth of kids, and a few others during winter. Despite the unavoidable uncertainties in these large-scale population counts, the estimated trends at the global and national scales presented in this work are likely to reflect the actual population dynamics, as the methods used to count the animals have remained constant over time (Jacobson et al. 2004).

If we consider the population dynamics of Alpine ibex on a larger temporal scale, considering that 150 years ago only a few hundred individuals survived in a single area (Grodinsky & Stüwe 1987), it is clear that the species has recovered and its total abundance has increased. However, the dynamics of the recent decades are harder to interpret. Although the global Alpine ibex population appears to have been stable over the last decade, we observed positive trends in Switzerland and Italy, while it was not possible to draw reliable conclusions about the trends for the other European countries (Fig. 3 and Table 1). This does not mean that the number of Alpine ibex in France, Austria, Germany and Slovenia did not change in recent years, but that the lack of available census data in many years, and the consequent uncertainty around the estimates, does not allow us to discuss the dynamics of the species in these countries.

In Switzerland and Austria, Alpine ibex are hunted to regulate the population size of colonies. The population dynamics of Alpine ibex in this country are therefore influenced by management decisions. Before our study (1990-2004), the number of Alpine ibex in Switzerland showed a marked decline (Source: Swiss Federal Office for the Environment BAFU-FOEN), probably due to a combination of hunting pressure (hunting is regulated by the ORES Act of 30 April 1990) and harsh winters. The hunting rate was deliberately reduced from 1999-2000 onwards as a consequence of this decline (BAFU-FOEN and Iris Biebach, personal communication), which may explain the increase observed in the timeframe of our study.

In Italy, it is more likely that the observed dynamics are the result of natural processes, as Alpine ibex hunting is forbidden (unfortunately, no data on estimated poaching pressure is available). However, the CIs around the estimate of the growth rate of the species in Italy are rather wide, which suggest caution in interpreting this result as a clear sign of population increase. A possible explanation for the increase of the numbers of Alpine ibex in Switzerland and Italy, despite the different management strategies, may be that several of the colonies in those countries have not yet reached carrying capacity. Indeed, studies performed in the Swiss colonies (Sæther et al. 2007, Bozzuto et al. 2019) as well as in the Gran Paradiso colony in Italy (Gran Paradiso National Park, unpublished data) have revealed relatively little density dependence. For the Swiss colony, this may partly be related to active management keeping the colonies below carrying capacity, but it may also be a signal that carrying capacity has not yet been reached. A detailed and rigorous analysis of the population dynamics of each colony was beyond the scope of this work. However, we show that the population growth rate of the colonies is positively related to the year of colony foundation (i.e. that the older colonies are growing less rapidly than the newer ones). This is as expected, since recently founded colonies typically grow exponentially in the first few years. However, the fact that Italy and

Switzerland showed positive trends, despite hosting some of the oldest colonies in the Alps, further corroborates the hypothesis that there is still potential for the colonies in those countries to grow. The timeframe of our study (i.e. 12 years, constrained by data availability) may be too limited to point out long-term population trends. The reasons driving the dynamics of the species in Italy and Switzerland would be worth exploring further in more detailed analyses.

Translocations of Alpine ibex for restocking purposes have taken place in Swiss and Italian colonies. Translocation was common practice in Switzerland: it is estimated that about 700 individuals were moved for restocking from 1950 to 2003, excluding founding events. Restocking is still happening sporadically today, although at a lower rate (40 individuals from 2004 to 2015; source: BAFU-FOEN). In Italy, if we exclude the founding of new colonies, translocations for restocking are not common. Given that most of the restocking events were done within the same country and comprised only a few individuals at a time, it is unlikely that they can have affected global abundance directly. Instead, it is possible that successful restocking events might have increased the growth rate of certain colonies, by reducing inbreeding levels (Hogg et al. 2006, Bozzuto et al. 2019). While it is possible that previous translocations have had a positive effect on population growth, it is not possible to disentangle their effects within the framework of this review, as translocations happened in different years for different colonies, and any genetic effects are likely to be delayed by several years from the restocking events.

The high heterogeneity in the spatial resolution of the data at our disposal requires caution when visually interpreting our range map and comparing it with what was reported by previous updates (e.g. Aulagnier et al. 2008). However, spontaneous recolonisation of new areas does not seem to have happened in recent years, although the density of many populations has increased. This is in line with the extremely long recolonisation time required by Alpine ibex (Gauthier & Villaret 1990, Scillitani et al. 2012), and with the fact that spontaneous contact between separate Alpine ibex colonies is unlikely to occur without human intervention, particularly for populations that are far apart. On the other hand, in areas where the Alpine ibex population density is higher, for example in the western Alps, several exchanges between populations have been observed (Groupe National Bouquetin France, personal communication), and in Switzerland at least one colony has become established through natural dispersal (Lukas Keller, personal communication).

CONCLUSION

In conclusion, the total abundance of the Alpine ibex in the Alps appears to have remained approximately stable or increased slightly in the last 12 years. However, variation in population trends between countries should be monitored in detail, as it may be a signal of different population dynamics in different areas of the species' range. The isolation of the colonies, combined with low recolonisation rates; extremely low genetic variability (Biebach & Keller 2010) that may lead to inbreeding depression (Brambilla et al. 2015), increased disease susceptibility (Brambilla et al. 2018) and reduced growth rate of colonies (Bozzuto et al. 2019); and local crashes or extinctions due to disease outbreaks are closely linked issues and continue to justify conservation action for the Alpine ibex. Moreover, the effect of climate change on this species has not yet been fully understood as different studies have reported different effects on population parameters (e.g. Pettorelli et al. 2007, Büntgen et al. 2014). However, concerns have been raised about increases in temperature and consequent behavioural changes (Mason et al. 2017), and the likely effects of climate change on population dynamics (Jacobson et al. 2004, Pettorelli et al. 2007, Mignatti et al. 2012). A better knowledge of the immunogenetics mechanisms and of the effect of environmental changes on the dynamics of the species are necessary to monitor its status. The underlying base for all these analyses is the availability of continuous data on the dynamics of each population.

Our synthesis highlights the fact that efforts to monitor the size and dynamics of Alpine ibex populations are not homogeneous among different Alpine countries, resulting in high levels of uncertainty around population size estimates for many colonies. This uncertainty hinders the reliable estimation of population trends at the colony and national levels, and therefore the correct assessment of the conservation status of the Alpine ibex in important sectors of its Alpine range. We therefore recommend increasing the long-term monitoring efforts on Alpine ibex in all Alpine countries; organising yearly total block counts in all colonies in the same season where possible; and, ideally, agreeing on a common monitoring protocol for all European Alpine ibex colonies. We believe that such a goal, while ambitious, is achievable, following the example of countries such as Switzerland, where standardised yearly counts are already in place. For the ongoing conservation of the Alpine ibex, it may be advantageous to exploit the transalpine collaboration platforms that already exist, such as the GSE-AIESG and the Large Carnivores, Wild Ungulates and Society Working Group (WISO) of the Alpine Convention for its implementation and coordination.

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REFERENCES

Apollonio M, Giacometti M, Lanfranchi P, Lovari S, Meneguz PG, Molinari P et al. (2009) Piano di conservazione, diffusione e gestione dello stambecco sull'arco Alpino italiano. Provincia di Sondrio.

Aulagnier S, Kranz A, Lovari S, Jdeidi T, Masseti M, Nader I, de Smet K, Cuzin F (2008) *Capra ibex*. IUCN Red List of Threatened Species. Version 2013.1.

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67: 1-48.

Biebach I, Keller LF (2010) Inbreeding in reintroduced populations: the effects of early reintroduction history and contemporary processes. *Conservation Genetics* 11: 527-538.

Bozzuto C, Biebach I, Muff S, Ives AR, Keller LF (2019) Inbreeding reduces long-term growth of Alpine ibex populations. *Nature Ecology & Evolution* 3: 1359-1364.

Brambilla A, Biebach I, Bassano B, Bogliani G, von Hardenberg A (2015) Direct and indirect causal effects of heterozygosity on fitness-related traits in Alpine ibex. *Proceedings of the Royal Society of London B: Biological Sciences* 282: 20141873.

Brambilla A, Keller L, Bassano B, Grossen C (2018) Heterozygosity–fitness correlation at the major histocompatibility complex despite low variation in Alpine ibex (*Capra ibex*). *Evolutionary Applications* 11: 631-644.

Büntgen U, Liebhold A, Jenny H, Mysterud A, Egli S, Nievergelt D, Stenseth NC, Bollmann K (2014) European springtime temperature synchronises ibex horn growth across the eastern Swiss Alps. *Ecology Letters* 17: 303-313.

Carmignola G, Stefani P, Gerstgrasser L (2006) 6° Rapporto rogna sarcoptica. Provincia autonoma di Bolzano, Ufficio caccia e pesca.

EEA (2018) Corine Land Cover (CLC) 2018, Version 20b2. Release date: 21-12-2018. European Environment Agency. https://land.copernicus.eu/pan-european/corine-land-cover/clc2018

Cregut-Bonnoure E (1992) Dynamics of bovid migration in western Europe during the middle and late Pleistocene. *Courier Forschungsinstitut Senckenberg* 153: 177-185.

De Danieli C, Sarasa M (2015) Population estimates, density-dependence and the risk of disease outbreaks in the Alpine ibex *Capra ibex*. *Animal Biodiversity and Conservation* 38: 101-119.

Garnier A, Gaillard JM, Gauthier D, Besnard A (2016) What shapes fitness costs of reproduction in long-lived iteroparous species? A case study on the Alpine ibex. *Ecology* 97: 205-214.

Gauthier D, Villaret JC (1990) La réintroduction en France du bouquetin des Alpes. *Revue d'Écologie (La Terre et La Vie)* 5: 97-120.

Giacometti M (1991) Beitrag zur Ansiedlungsdynamik und aktuellen Verbreitung des Alpensteinbockes (*Capra i. ibex* L.) im Alpenraum. *Zeitschrift für Jagdwissenschaft* 37: 157-173.

Grignolio S, Parrini F, Bassano B, Luccarini S, Apollonio M (2003) Habitat selection of adult males of Alpine ibex, *Capra ibex ibex*. *Folia Zoologica* 52: 113-120.

Grignolio S, Rossi I, Bertolotto E, Bassano B, Apollonio M (2007) Influence of the kid on space use and habitat selection of female Alpine ibex. *Journal of Wildlife Management* 71: 713-719.

Grodinsky C, Stüwe M (1987) With lots of help alpine ibex return to their mountains. *Smithsonian* 18: 68-77.

Grossen C, Keller LF, Biebach I, Croll D (2014). Introgression from domestic goat generated variation at the major histocompatibility complex of Alpine ibex. *PLOS Genetics* 10:e1004438.

Grossen C, Biebach I, Angelone-Alasaad S, Keller LF, Croll D (2018) Population genomics analyses of European ibex species show lower diversity and higher inbreeding in reintroduced populations. *Evolutionary Applications* 11: 123-139.

Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33: 1-22. http://www.jstatsoft.org/v33/i02/

Hogg JT, Forbes SH, Steele BM, Luikart G (2006) Genetic rescue of an insular population of large mammals. *Proceedings of the Royal Society B: Biological Sciences* 273: 1491-1499.

Jacobson AR, Provenzale A, von Hardenberg A, Bassano B, Festa-Bianchet M (2004) Climate forcing and density dependence in a mountain ungulate population. *Ecology* 85: 1598-1610.

Kazanskaya EY, Kuznetsova MV, Danilkin AA (2007) Phylogenetic reconstructions in the genus *Capra* (Bovidae, Artiodactyla) based on the mitochondrial DNA analysis. *Russian Journal of Genetics* 43: 181-189.

Largo E, Gaillard JM, Festa-Bianchet M, Toïgo C, Bassano B, Cortot H et al. (2008) Can ground counts reliably monitor ibex *Capra ibex* populations. *Wildlife Biology* 14: 489-500.

Manceau V, Després L, Bouvet J, Taberlet P (1999) Systematics of the genus *Capra* inferred from mitochondrial DNA sequence data. *Molecular Phylogenetics and Evolution* 13: 504-510.

Mick V, Le Carrou G, Corde Y, Game Y, Jay M, Garin-Bastuji B (2014) *Brucella melitensis* in France: persistence in wildlife and probable spillover from Alpine ibex to domestic animals. *PLoS One 9(4)*, e94168.

Mason TH, Brivio F, Stephens PA, Apollonio M, Grignolio S (2017) The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species. *Behavioral ecology* 28: 908-918.

Mignatti A, Casagrandi R, Provenzale A, von Hardenberg A, Gatto M (2012) Sex- and age-structured models for Alpine ibex *Capra ibex ibex* population dynamics. *Wildlife Biology* 18: 318-332.

Pettorelli N, Pelletier F, von Hardenberg A, Festa-Bianchet M, Côté SD (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. *Ecology* 88: 381-390.

Pidancier N, Jordan S, Luikart G, Taberlet P (2006) Evolutionary history of the genus *Capra* (Mammalia, Artiodactyla): discordance between mitochondrial DNA and Y-chromosome phylogenies. *Molecular Phylogenetics and Evolution* 40: 739-749.

QGIS Development Team (2016) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2016) *R: a Language and Environment for Statistical Computing.* R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Scillitani L, Sturaro E, Menzano A, Rossi L, Viale C, Ramanzin M (2012). Post-release spatial and social behaviour of translocated male Alpine ibexes (*Capra ibex ibex*) in the eastern Italian Alps. *European Journal of Wildlife Research* 58: 461-472.

Sæther BE, Lillegård M, Grøtan V, Filli F, Engen S (2007). Predicting fluctuations of reintroduced ibex populations: the importance of density dependence, environmental stochasticity and uncertain population estimates. *Journal of Animal Ecology* 76: 326-336.

Stüwe M, Nievergelt B (1991) Recovery of alpine ibex from near extinction: the result of effective protection, captive breeding, and reintroductions. *Applied Animal Behaviour Science* 29: 379-387.

Stüwe M, Scribner KT (1989) Low genetic variability in reintroduced alpine ibex (*Capra ibex ibex*) populations. *Journal of Mammalogy* 70: 370-373.

Tosi G, Scherini G, Apollonio M, Ferrario G, Toso S, Pacchetti G, Guidali F (1986) Modello di valutazione ambientale per la reintroduzione dello stambecco (*Capra ibex ibex*). *Supplemento alle ricerche di biologia della selvaggina* 77: 5-77.

Wiersema G, Gauthier D (1990) Status and aspects of reintroduction and management of the Ibex in the Alps. *Travaux Scientifiques du Parc National de la Vanoise* 18: 235-252.

Wood SN (2003) Thin plate regression splines. *Journal of the Royal Statistical Society: Series B Statistical Methodology* 65: 95-114.

Figures

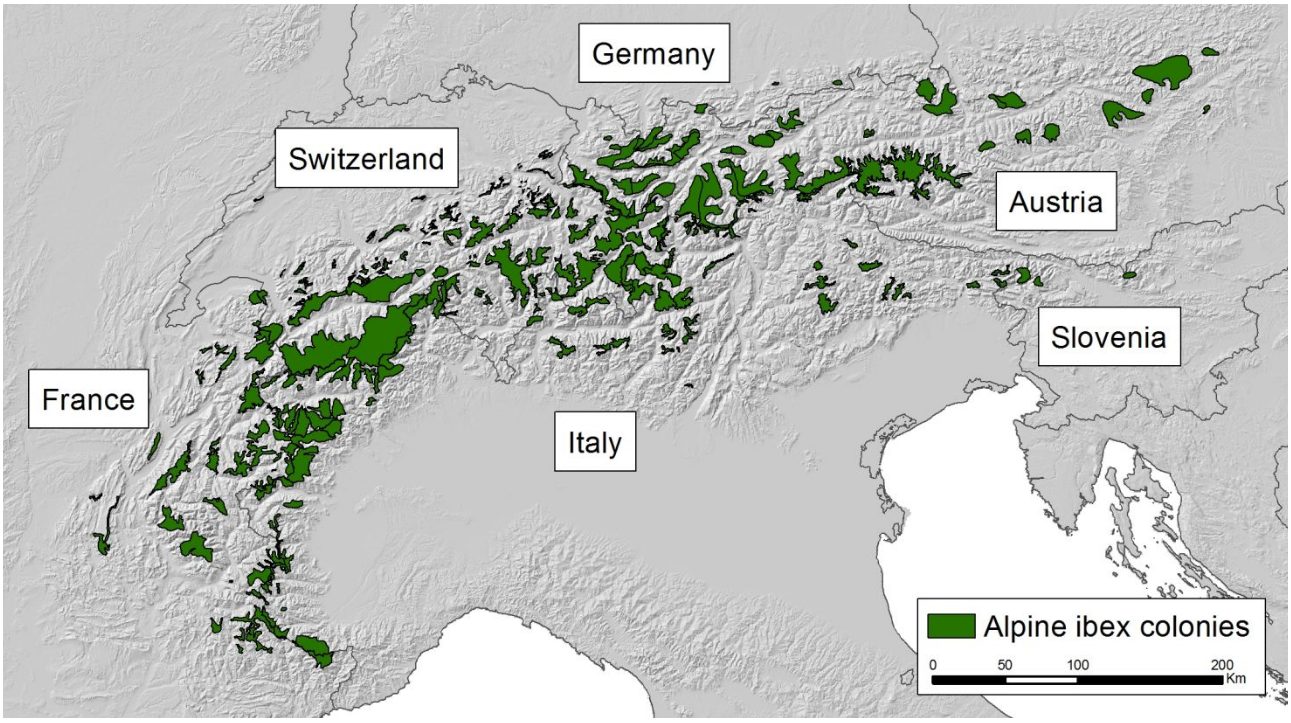


Fig. 1. Geographic range map of the 178 Alpine ibex *Capra ibex* populations in Europe. For a summary of all colonies where numbers of Alpine ibex have been counted, see Appendix S2.

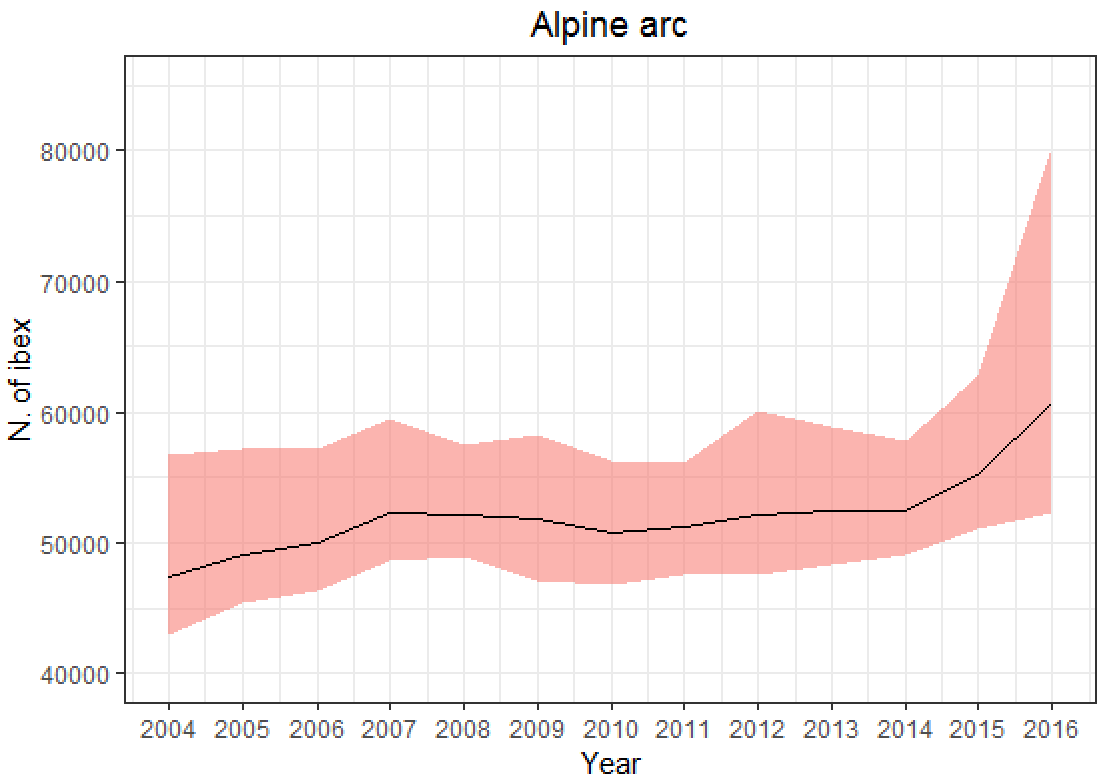


Fig. 2. Estimates of the trend in numbers of Alpine ibex present on the Alps from 2004 to 2016. The black line represents the estimated number and the filled area indicates the Credible Intervals extracted by Bayesian hierarchical Poisson models. The y-axis lower limit was set to 40000 for a better view of the trend.

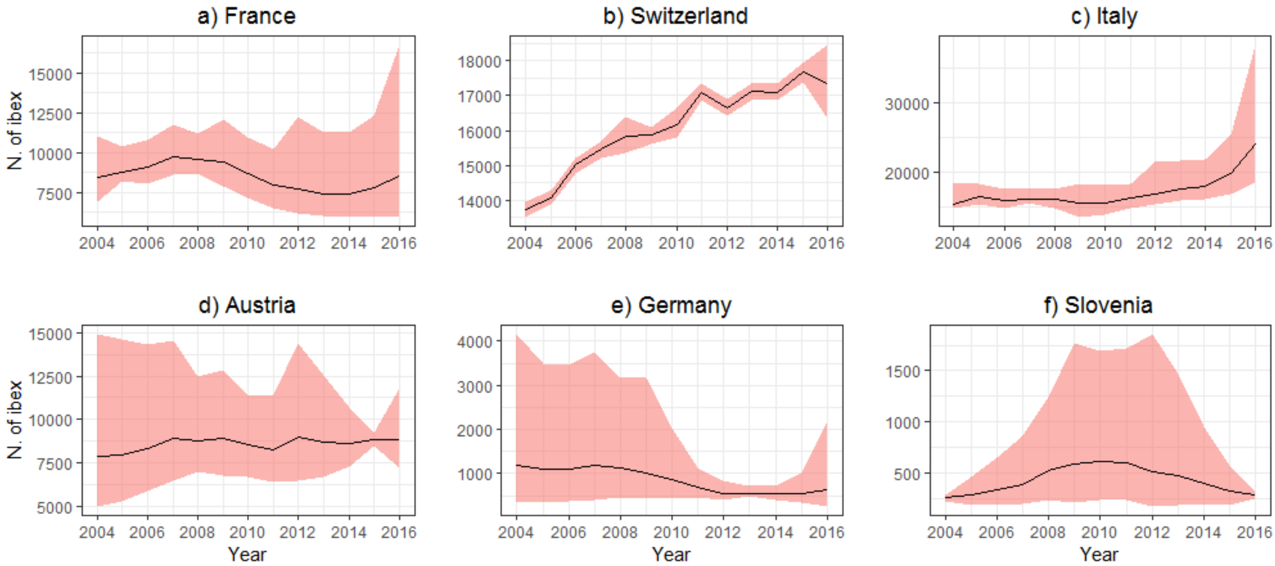


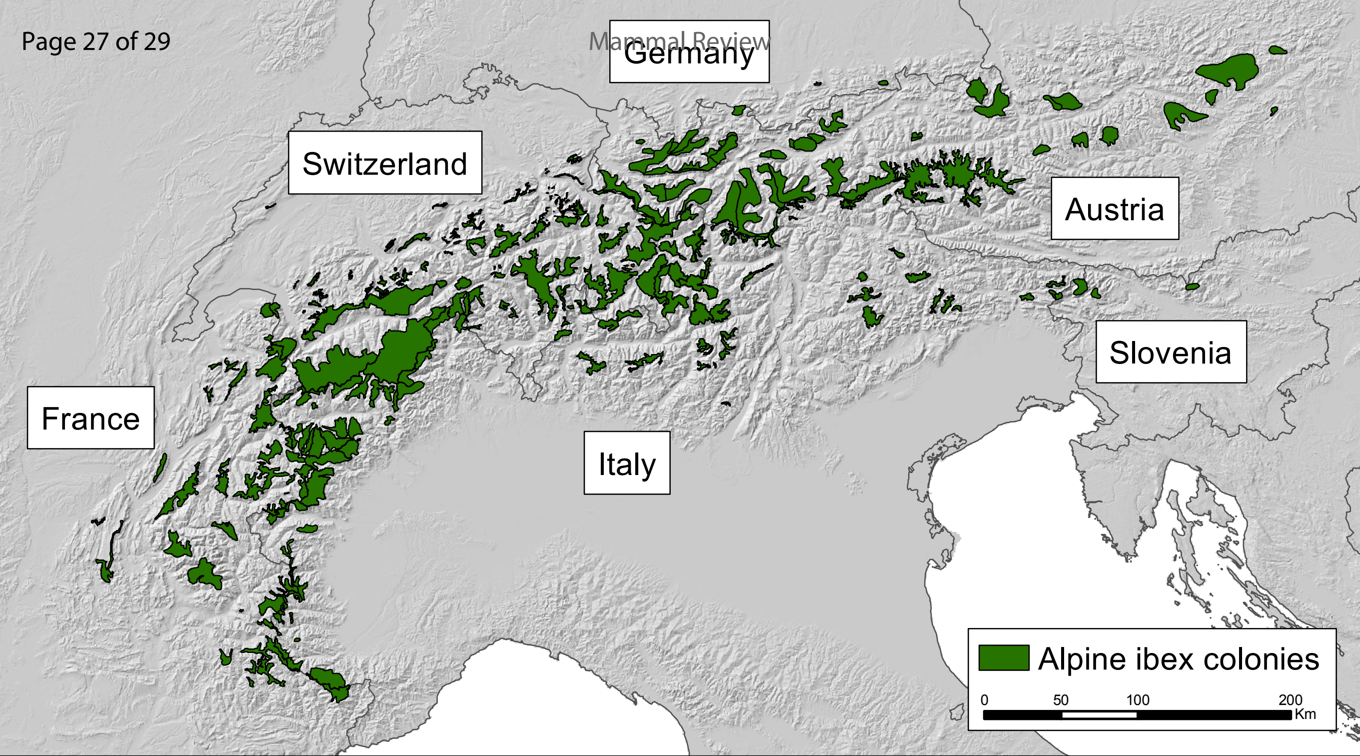
Fig. 3. Estimates of the trend in numbers of Alpine ibex present in Alpine countries from 2004 to 2016. The black line represents the estimated number and the filled area the Credible Intervals extracted by Bayesian hierarchical Poisson models. The y-axis limits differ for each plot to favour readability of the trends.

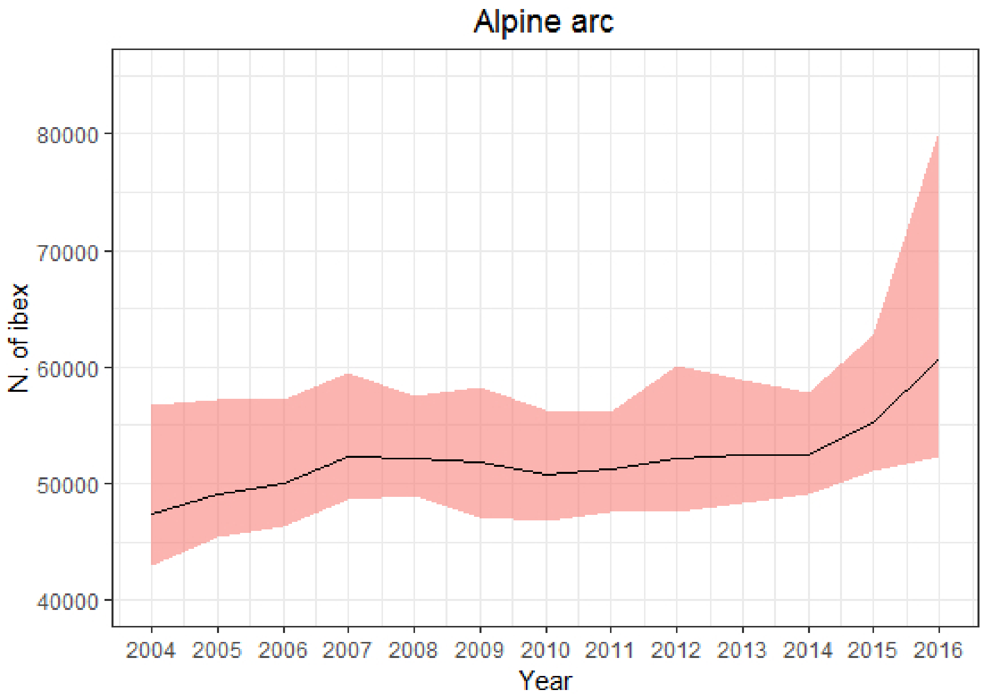
SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1 Description of the different management regulations in the European countries hosting Alpine ibex populations.

Appendix S2 Interactive map showing all the populations considered in the study, the species' geographic range, and the location, density, and number of Alpine ibex counted from 2004 to 2016.


Germany
Switzerland
Austria
France
Slovenia
Italy
Alpine ibex colonies
0
50
100
200
Km



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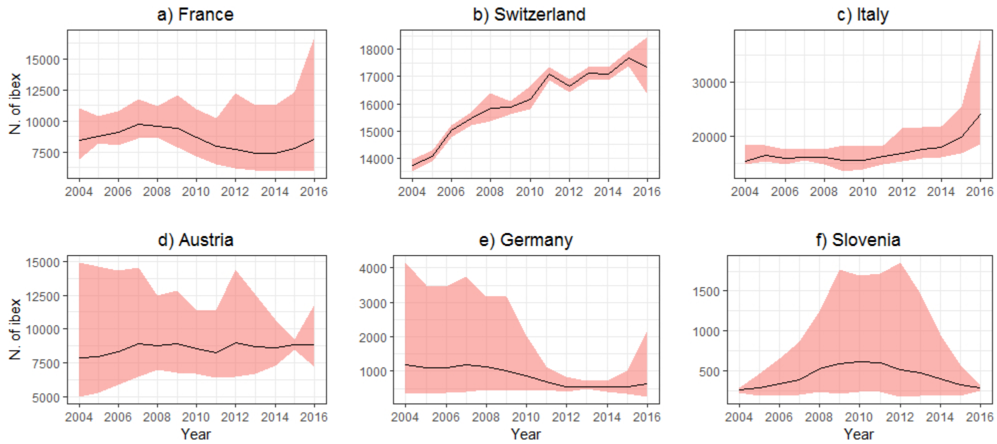

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