

Recovery of large carnivores in Europe's modern human-dominated landscapes

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CONSERVATION

Recovery of large carnivores in Europe's modern human-dominated landscapes

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The conservation of large carnivores is a formidable challenge for biodiversity conservation. Using a data set on the past and current status of brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), gray wolves (*Canis lupus*), and wolverines (*Gulo gulo*) in European countries, we show that roughly one-third of mainland Europe hosts at least one large carnivore species, with stable or increasing abundance in most cases in 21st-century records. The reasons for this overall conservation success include protective legislation, supportive public opinion, and a variety of practices making coexistence between large carnivores and people possible. The European situation reveals that large carnivores and people can share the same landscape.

Large carnivores are among the most controversial and challenging group of species to conserve in our modern and crowded world. There is a deeply rooted hostility to these species in human history and culture, because of perceptions of their negative impacts on human livelihoods (1). Large carnivore abundance and distribution have historically been reduced (2), and their present conservation has become intertwined with broader emotional, political, and socioeconomic issues that further complicate this challenge (3). In addition, large carnivores live at low densities and have large spatial requirements (4). Accordingly, the conservation of viable large carnivore populations needs to be planned and coordinated on very wide scales, often spanning many intra- and international borders [i.e., requiring transboundary management (5)].

The main debate around large carnivore conservation is whether there is enough suitable space

left for viable and ecologically functional populations (6). As the two main drivers of the current biodiversity crisis—human overpopulation and overconsumption—show no sign of reducing, an intuitive forecast could be that large carnivores will persist only in highly managed protected areas (with regular translocations being made to achieve artificial connectivity) or in some remote and uninhabited wilderness areas. This approach derives conceptually from the North American wilderness model that separates people and nature and that has further been adopted in many Asian, African, and neotropical countries (6) (“keeping people and predators apart,” the separation model). The ultimate expression of this approach lies in the southern African propensity to fence protected areas (6). The alternative model, “allowing people and predators together” (coexistence model), following a landscape-scale conservation approach, has rarely been given proper consideration, probably because

it has been deemed a priori to fail because of the existing conflicts between large carnivores and humans. This dichotomy of large carnivore conservation models is analogous to the land-sharing versus land-sparing debate, which is ongoing in a wider biodiversity conservation context (7).

We compiled data about the status (i.e., current and past occurrence and abundance) of large carnivores [brown bears (*Ursus arctos*), Eurasian lynx (*Lynx lynx*), gray wolves (*Canis lupus*), and wolverines (*Gulo gulo*)] in Europe (8). We show that the European continent (considering all continental European countries excluding Belarus, Ukraine, and Russia) is succeeding in maintaining, and to some extent restoring, viable large carnivore populations on a continental scale (Fig. 1 and fig. S1). All mainland European countries except for Belgium, Denmark, the Netherlands, and Luxembourg have a permanent and reproducing occurrence of at least one species of large carnivore (Fig. 1). The total area with a permanent presence of at least one large carnivore species in Europe covers 1,529,800 km² (roughly one-third of mainland Europe), and the area of occasional presence is expanding, as the presence of solitary dispersing wolves has been confirmed in both Denmark and Belgium in recent times.

Brown bears presently occur permanently in 22 countries (485,400 km²) and can be clustered into 10 populations, most of which are native populations (tables S1 to S3). Eurasian lynx presently occur permanently in 23 countries (813,400 km²) and can be clustered into 11 populations, five of them being native populations (tables S5 to S7). Wolves currently occur permanently in 28 countries (798,300 km²) and can be clustered into 10 populations, which are all native (tables S9 to S11). Wolverines, however, are only found in the three Fennoscandic countries, and they permanently occur over a total of 247,900 km² in two populations (tables S13 to S15). Because of the limited biogeographic distribution of wolverines, Fennoscandia is the only region containing all four large carnivore species in Europe (171,500 km²), and could be considered as a large-carnivore hot spot together with southeastern Europe (Dinaric, Carpathian, and Balkan regions) and the Baltics (fig. S2). Three large carnivore species overlap over 593,800 km² in Europe (fig. S2).

Overall, Europe hosts several large and stable populations on the order of thousands of individuals, many medium-sized and increasing populations that number in the hundreds of individuals, and a few small and declining populations with a few tens of individuals. Interestingly, none of the medium or large populations are declining. Brown bears are the most abundant large carnivore in Europe, with an estimated total number around 17,000 individuals, and all population ranges have

been relatively stable or slightly expanding (table S2). Wolves are the second most abundant species, with an estimated total number larger than 12,000 individuals (table S10). Most populations have been increasing or stable during recent years, although the Sierra Morena population (Spain) is on the brink of extinction, with only one pack detected in 2010 (9). In recent years, the larger Iberian population has an uncertain trend, although it seems stable, and the Karelian population has declined (9). The estimated total number of Eurasian lynx is around 9000 individuals (table S6), and most populations have generally been stable in the past decade, although most of the reintroduced populations appear to have stagnated at relatively small sizes, and the Vosges-Palatinian and Balkan lynx populations have declined (9). Finally, the estimated total number of wolverines is 1250 individuals, and both populations are increasing (table S14). Details on large carnivore monitoring methods are given in tables S4, S8, S12, and S16 and (9).

All four large carnivore species are persisting in human-dominated landscapes (fig. S3) and largely outside protected areas. The mean \pm SD human density in areas of permanent large carnivore presence is 19.0 ± 69.9 inhabitants/km² (range: 0 to 1651) for brown bears; 21.8 ± 73.8 inhabitants/km² (range: 0 to 2603) for lynx; 36.7 ± 95.5 inhabitants/km² (range: 0 to 3050) for wolves; and 1.4 ± 5.7 inhabitants/km² (range: 0 to 115) for wolverines (fig. S3). These figures suggest species-specific sensitivities of large carnivores to humans, with wolves being most successful in adapting to human-dominated landscapes (fig. S3). Wolverines are somewhat special, because their distribution is constrained by climatic conditions, which restricts them to northern and high-altitude areas, which have low human population densities (10).

These figures permit cautious optimism for the occurrence, abundance, and trends for large carni-

vores in Europe. The general picture emerging from the current status of large carnivores in Europe is that these species have shown the capacity to survive in human-dominated landscapes, representing an often underappreciated conservation success story. Having high numbers of large carnivores in such landscapes is not exclusive to Europe [the United States has abundant populations of black bears (*Ursus americanus*) and mountain lions (*Puma concolor*)]; however, the largest species, brown bears and wolves, occur in Europe with much higher human densities. For example, Europe hosts twice as many wolves (>11,000) as the contiguous United States (~5500 wolves (11)), despite being half the size (4.3 million km² versus 8 million km²) and more than twice as densely populated (97 inhabitants/km² versus 40 inhabitants/km²).

We believe that the alternative view to the coexistence model (i.e., the separation model), which argues that the largest predators can only survive in protected areas or wilderness, is a consequence of former policy goals to exterminate these species (12). However, our results underline that if the separation model had been applied in Europe, there would hardly be any large carnivore populations at all, because most European protected areas are too small to host even a few large carnivore reproductive units (13).

Whereas large carnivores do not permanently occur in the areas of highest human density in Europe, they have shown an ability to recolonize areas with moderate human densities if they are allowed, and to persist in highly human-dominated landscapes and in the proximity of urban areas (14, 15) in highly fragmented landscapes consisting of forest-farmland mosaics or even agro-ecosystems. Our results are not the first to reveal that large carnivores can coexist with people (16–18), but they show that the land-sharing model for large carnivores (coexistence model) can be successful on a continental scale.

The reasons for the success of large carnivores in Europe range from coordinated legislation shared by many European countries (19, 20) to context-specific management practices and institutional arrangements. Since the end of World War II, Europe has benefited from stable political institutions ensuring proper law enforcement. The post-communist transition in Eastern European countries was not generally associated with institutional collapse, with the exception of some Balkan countries. This stability created the conditions for securing land tenure and associated rights for activities such as forestry and hunting, which are preconditions for the development of sustainable practices. The rise of environmental movements in the 1970s provided the motivation for various pan-European legislative agreements to emerge that served to promote biodiversity conservation. For example, the Bern Convention, administered by the Council of Europe, covers all countries included in this report, and the Habitats Directive covers all 20 European Union member states with a permanent occurrence of large carnivores. Consequently, the four large carnivore species examined here enjoy some degree of legal protection in all European countries. Large carnivores have also benefited from the socioeconomic changes over the past four decades that led to an improvement in habitat quality. For example, Europe again hosts large populations of wild ungulates (21), which can sustain large carnivore populations. The impact of human land-use activities has also been declining in many areas because of a widespread exodus from rural areas and the associated abandonment of agricultural land (22). These broad patterns are further accompanied by a variety of local, cultural, or regulatory practices making coexistence between large carnivores and people possible (15, 23). One important prerequisite has been to maintain and revive traditional livestock protection measures

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(livestock-guarding dogs, night corrals, and sheepherds), as well as to invest in new techniques (electric fences) as an important nonlethal tool to minimize large carnivore depredation on livestock (24).

The most severe challenges for large carnivore conservation are in countries where large carnivores have previously been extirpated, where the adaptations for coexistence have been lost, or where husbandry practices have evolved toward new production schemes. In such contexts, the return of large carnivores can trigger social conflicts. For example, poaching enjoys social acceptance in rural areas of Norway (25), limits the recovery of wolves in Scandinavia (26), and eradicated a reintroduced bear population in Austria (27). In these areas, the practical challenges and economic impacts of carnivore conservation have escalated into social conflicts, where the carnivores have become symbols of wider political divisions between rural and urban populations and between individuals and groups with fundamentally different value orientations and interests.

At present, there is a conjuncture between many policy areas combined with a generally supportive public opinion, so that the positive forces have been prevailing. However, the underlying negative forces are still present and could reemerge as a result of ecological, social, political, or economic changes. There is a need to monitor both the ecological situation and sociopolitical climate to ensure that the current trends are maintained.

The European experience offers hope for wildlife conservation in human-dominated landscapes and is relevant to other areas of the world. Although developing countries may lack many of the institutions and capacities that have enabled large carnivore recovery in Europe, there are other examples of large carnivores persisting and recovering in human-dominated landscapes and even in cities (17, 28, 29). Clearly, the presence of large carnivores in human-dominated ecosystems is associated with modified ecological conditions that deviate from conditions in areas with little human activity. However, the fact that such species

can persist in these novel ecosystems encourages optimism for the conservation of larger and more connected large carnivore populations.

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SUPPLEMENTARY MATERIALS

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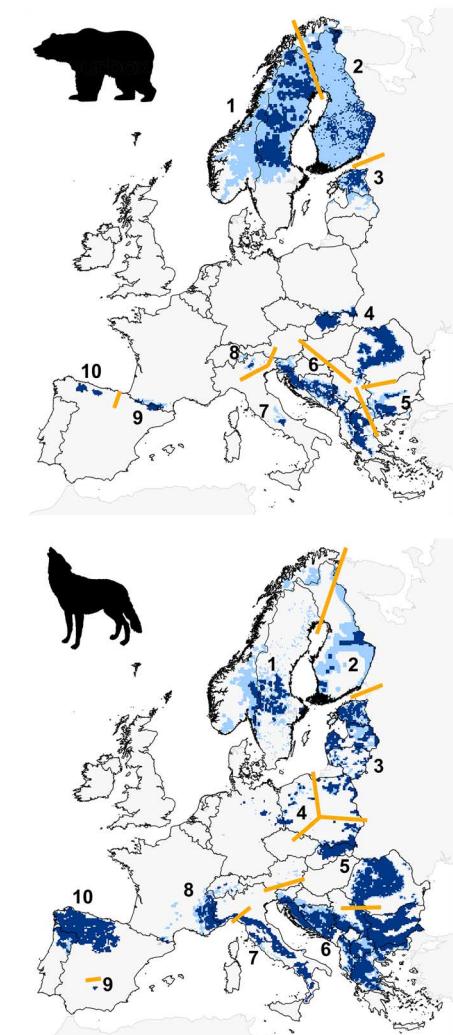


Fig. 1. Distribution of large carnivores in Europe in 2011. Brown bears (top left), Eurasian lynx (top right), gray wolves (bottom left), and wolverines (bottom right). Dark blue cells indicate areas of permanent occurrence, and light blue cells indicate areas of sporadic occurrence. Numbers refer to population identifications in tables S1 to S16. Orange lines indicate boundaries between populations.

Supplementary Materials for

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References (30–258)

Supplementary Materials:

Materials and Methods: We collected standardized information on the status (abundance and distribution range) of large carnivores along all countries comprising Europe (excluding Russia, Belarus and Ukraine) through a detailed questionnaire sent to members of the Large Carnivore Initiative for Europe (LCIE; a specialist group of the IUCN's Species Survival Commission; www.lcie.org) and other knowledgeable experts in 2012. LCIE members compiled the most up to date and accurate data from their country. This was mainly built on accessing results from national and regional governmental large carnivore monitoring activities and official statistics, but also included results from ongoing research and conservation projects (e.g. LIFE projects). Some additional material was compiled from a literature review considering recent reports or publications and/or by further contacting experts or authorities via e-mail or telephone. The compiled information was presented to the EU Commission in 2013 (9) and is the basis for this study. We did not cover the very small countries (e.g. Lichtenstein, Andorra). The designation of Kosovo in tables S1-S16 is without prejudice to positions on status, and is in line with UNSCR 1244/99 and the ICJ Opinion on the Kosovo declaration of independence.

Species distribution

Large carnivore distribution range was separated into two categories using the following criteria: (i) permanent presence, where a cell was occupied by the species at least 50% of the time over 3 years or more and/or where there was either confirmed reproduction or the presence of resident adult females and, (ii) sporadic occurrence, areas of occasional presence (e.g. dispersers) and/or no reproduction. For the latter category, we acknowledge that the ability of monitoring programs to detect, for instance, dispersing individuals will vary greatly depending on the effort invested. We compiled distribution maps for the four large carnivores pooling all data available during the last 3–5 years on a 10 x 10 km grid basis using ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA). We selected this grid size because all these species usually have large spatial requirements and an average home range of a lynx (e.g. (30-32)), wolf (e.g. (33, 34)), bear (e.g. (35, 36)) or wolverine (e.g. (37, 38)) is likely to cover several grid cells in most of the European contexts they occur. Maps were compiled at two different spatial levels, on a country basis and on a European level. Overlapping cells of transboundary populations were assigned to the country with the higher level of occupancy, e.g. if a transboundary cell was defined to be of permanent presence by one country and of sporadic presence by the other country, the cell was given the status of permanent presence.

Species abundance

We reported population estimates (estimated number of individuals) for all large carnivore populations by compiling the most recent country census data. We calculated distribution ranges, considering both permanent and sporadic occurrence, based on the number of cells on a population level with population borders defined according to (39). However, because population boundaries have not been formally fixed, assignment of cells to one or the other population remains open to interpretation for sporadic occurrence at contact zones. The results from this survey were compared to data on large carnivores at their lowest extend from WWII to the 1970s (references in tables S1, S5, S9, S13) even for populations that reached a lowest extend before WWII (such as brown bears in Scandinavia). Because actual and historical estimates are derived from different monitoring methods and are not immediately comparable, change in estimates is shown by a rough multiplying factor in tables S2, S3, S6, S7, S10, S11, S14 and S15. For each large carnivore species we estimated the range of human densities in its range by converting the GEOSTAT 1 x 1 km human density map (40) to the same 10 x 10 km grid.

Estimating the number of large carnivores in a given area is always a difficult task even within a limited area and Europe shows a wide diversity of approaches that have been developed based on different ecological situations (e.g. the presence or absence of snow), different social situations (e.g. the extent to which hunters take part in the activity), different financial situations, and different behaviours of large carnivores. As a result, the quality of the census data reported by the different countries for the different species and the different populations varies dramatically. Overall, the small populations are subject to more intensive and costly monitoring methods than the larger populations where monitoring largely attempts to document presence or relative densities. The fact that all of the countries that are members of the European Union have reporting requirements under the Habitats Directive (19) motivates a fair degree of activity in most of the area (countries) considered in this study, and in some other countries wildlife management institutions are well developed. However, some of the countries in southern Europe have relatively poorly developed programs. The result is that in some countries methodology is based on systematic sampling using methods such as capture-recapture based on non-invasive genetic analysis of scats and hairs, whereas in other countries carnivore numbers may well be an educated guess. This high variability in the data implies that the population estimates may not be directly comparable between countries, populations or time periods. As a consequence, the estimates for a few large carnivore populations have decreased recently because of an improvement of census methodology (e.g. wolves in Slovenia and Bulgaria; bears in Eastern Balkan). Nevertheless, we are confident that our database constitutes the best available and most complete large-scale assessment of large carnivore population estimates in Europe that is possible at this point in time. Hereafter, we summarize the most common methods used to monitor large carnivore in Europe by

species. The detailed country- and species-specific information is available in a report to the European Commission (9).

Brown bear

In several countries, genetic methods that use non-invasively collected DNA (from scats or hairs) (41, 42) are an important component of bear monitoring (e.g. Norway, Sweden, Italy, Austria, France, Greece, Slovenia, FYR Macedonia) or are used to compliment or confirm data obtained by other methods (e.g. counts at feeding sites, snow tracking, counts of females with cubs and telemetry) (Croatia, Poland, Slovakia, Spain). In the countries without genetics and telemetry, absolute estimates are based on much weaker grounds. The small populations are generally subject to more intense and costly monitoring methods to precisely estimate population size (43), although the most closely monitored population is one of the largest, in Scandinavia (44). In hunted populations harvest data is used to identify population trends. Monitoring methods are further detailed for each country in table S4 with references in table S1.

Lynx

Lynx monitoring is usually based on a combination of various methods (45-50). Monitoring in the Scandinavian population is based on snow-tracking, harvest data, genetics (to separate close living females with cubs), and collection of livestock depredation cases, supported by telemetry and camera-trapping. In Finland (Karelian population), snow-tracking and telemetry are used. In Estonia, Latvia and Poland estimates are based on snow-tracking, supported by analysis of harvest bag data in Estonia and Latvia. In the Carpathians, monitoring and population estimates are based mainly on hunting ground counts, snow-tracking and expert assessments. For the Alpine, Jura and Vosges populations, camera-trapping (including capture-mark-recapture in reference areas and density extrapolation) is combined with the collection of different data sets validated using the criteria developed by the Status and Conservation of the Alpine Lynx Population (SCALP) project (51, 52). The same is true for the Balkan population and the Bavarian part of the Bohemian-Bavarian population. The basic monitoring methods for the Dinaric population are snow-tracking (all three countries), genetic sampling and guesstimates (Slovenia and Croatia). In the Bohemian and Harz region a variety of the methods is used including collection of signs, genetics and camera-trapping (53). Monitoring methods are further detailed for each country in table S8 with references in table S5.

Wolf

Wolf monitoring in Scandinavia is based on intensive snow tracking complemented with genetics and telemetry allowing for good estimates of annual number of reproductions, the total number of individuals, and even information on the inbreeding coefficient of

individual pack members (54-56). In the Finnish part of the Karelian population, monitoring is based on intensive snow tracking, telemetry and some genetic analysis. In the Baltics, harvest data, snow tracking and damage statistics are used for monitoring. The Central European Lowlands population is monitored by using snow tracking and other sign surveys in combination with genetics, camera trapping (Poland & Germany) and telemetry (Germany). In the Carpathian population monitoring is largely based on harvest and damage statistics and the collection of wolf signs by various interest groups including hunters and foresters, however the main method remains an interpretation of assessments made by the various hunting grounds where the methodology is somewhat unclear. The Dinaric-Balkan population spans the most national borders and thus is subject to the most diverse monitoring ranging from interviews with local people and expert assessments based on harvest data, damage reports, sign surveys, camera trapping, telemetry and genetics. The Italian peninsula population is also monitored through a mix of signs collected over varying time periods by various interest groups, damage reports and expert assessment. The Alpine wolf population is intensively monitored by genetics, confirmed damages, camera trapping, intensive snow tracking and sign surveys (57, 58). The Northwestern Iberian and Sierra Morena populations are monitored by rendezvous site mapping using sign surveys in combination with provoked howling censuses to confirm reproduction (59, 60). Monitoring methods are further detailed for each country in table S12 with references in table S9.

Wolverine

In both Sweden and Norway wolverines are surveyed annually in March–May by snow tracking and identification of natal dens which represent reproductions (37). Reproductions are registered based on observations of cub tracks, visual observation of cubs or documentation of den sites. Den sites are documented based on characteristics that can separate den sites from cache sites or day-beds. In both Norway and Sweden many of the sites are revisited during summer after snow melt to collect further evidence of reproduction. Norway also has an annual collection of scats based on snow-tracking using snow-scooters, harvest data and depredation reports. This survey aims to cover the entire wolverine range each year. Genetic methods are used to conduct capture-mark-recapture estimates of population size. The survey in Finland is based on snow-tracking and line-transects performed in winter which aim to estimate the total number of individuals in the population. See also table S13 and S16.

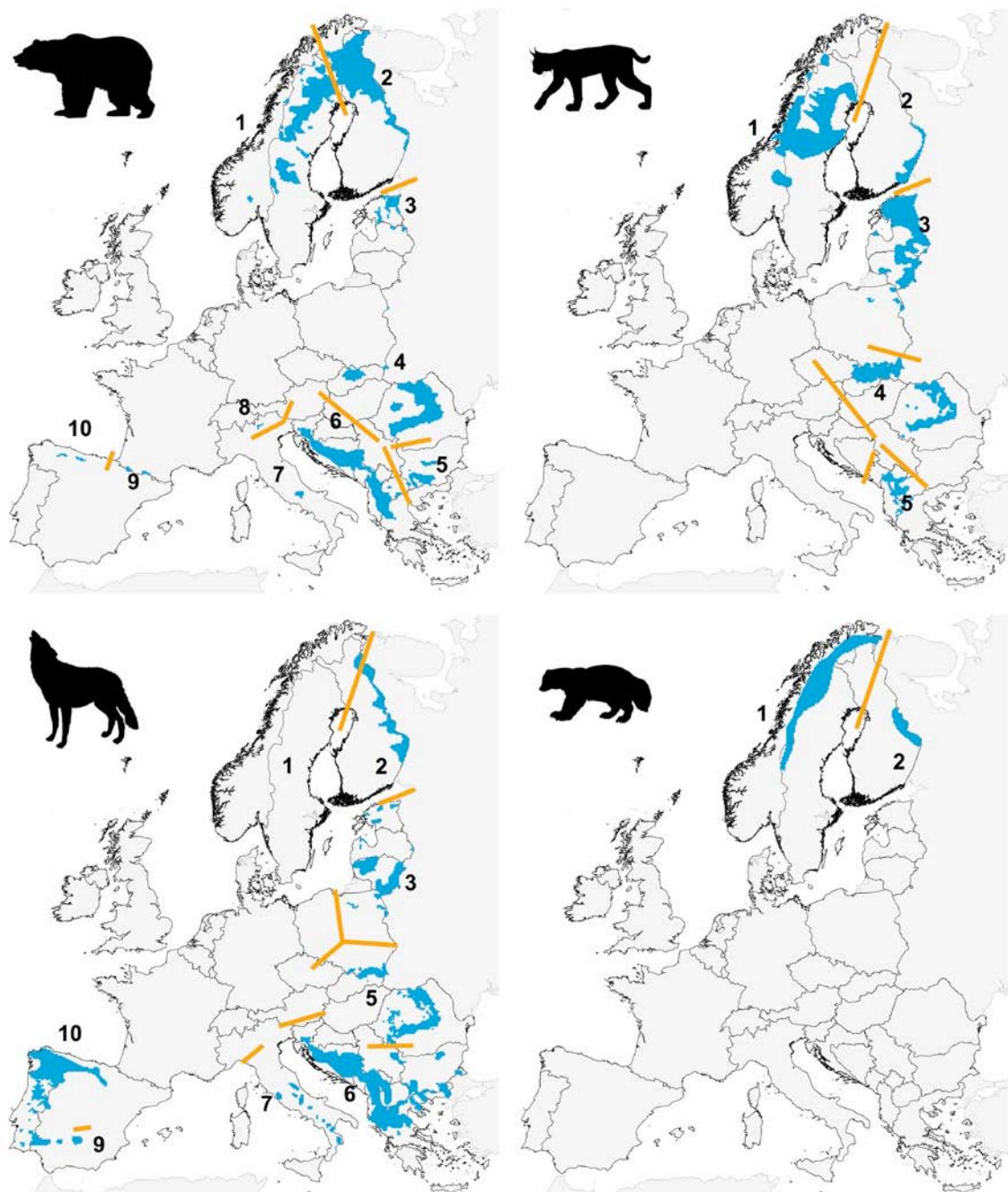


Fig. S1. Distribution of large carnivores in Europe at their lowest extend during the 1950–1970s. Brown bears (top left), Eurasian lynx (top right), grey wolves (bottom left) and wolverines (bottom right). Numbers refers to populations ID in tables S1-S16. Orange lines indicate boundaries between populations, which have been designated for the purpose of this analysis. Countries can have different criteria and time periods for the definition of cells with large carnivore presence.

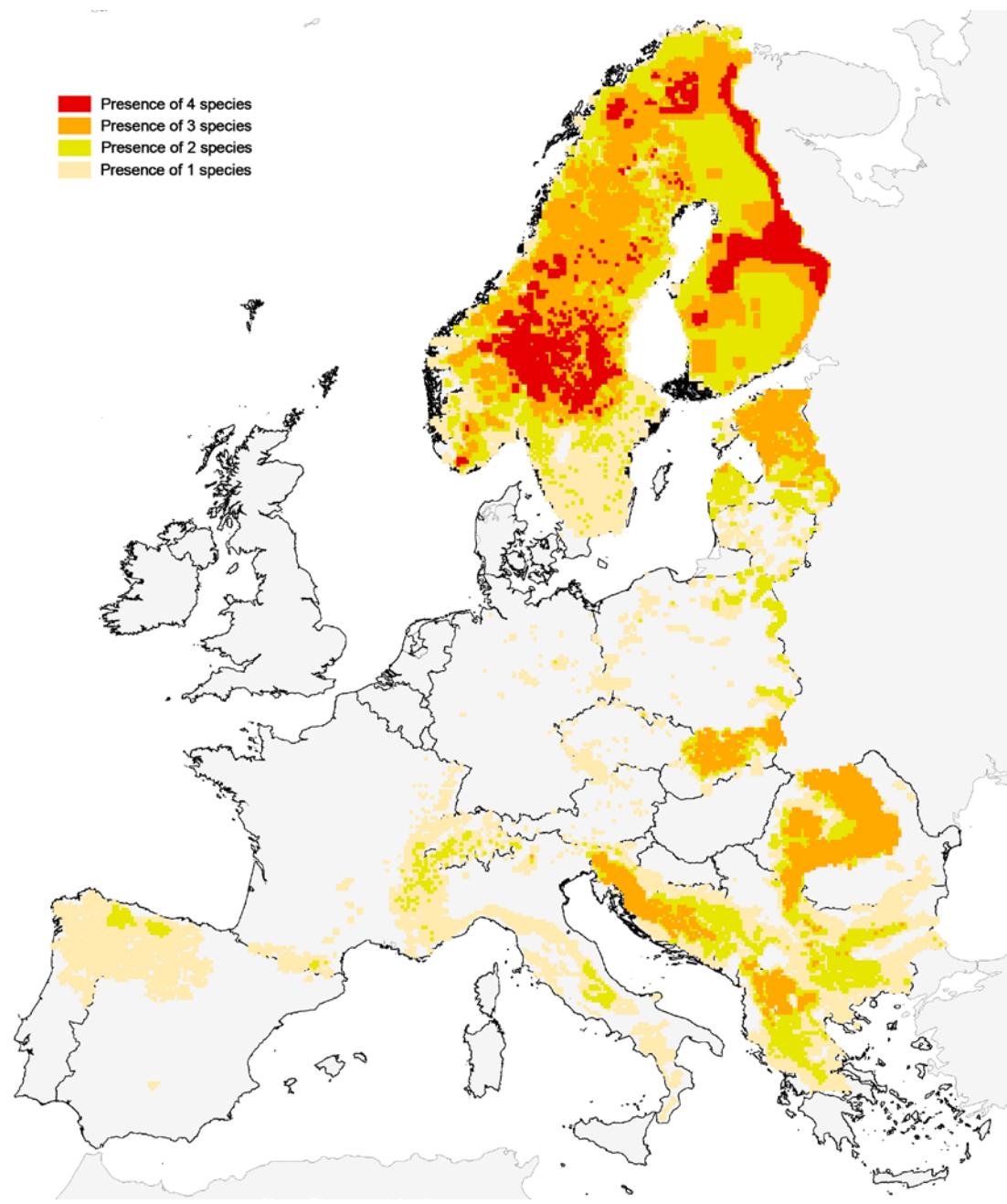


Fig. S2. Distribution of large carnivore hotspots in Europe in 2011. Both permanent and sporadic occurrences are used to show overlap between species distribution.

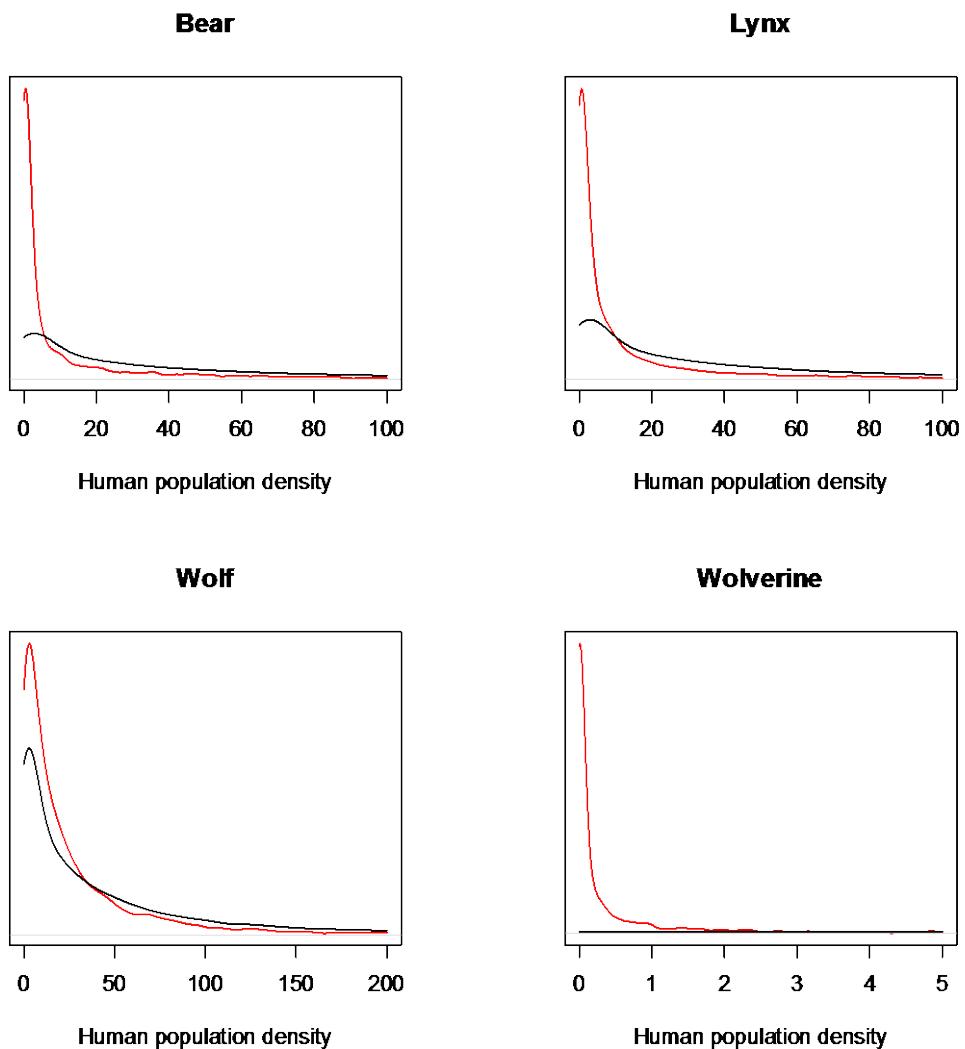


Fig. S3. Human population density in large carnivore permanent presence areas.

The red curve shows for each species the density distribution of human population densities (people / km²) for 10 x 10 km cells permanently occupied by a large carnivore species. We only used permanent cells (where the species breed). The black curve shows the density distribution of human population densities across all Europe (excluding United Kingdom).

Table S1. Brown bear population names, countries and literature references.

Populations have been designated for the purpose of this analysis according to (39). Literature refers to actual abundance and distribution data, monitoring methods, historical abundance and distribution data. Population data do not cover Belarus, Russia and Ukraine.

Population	Country	References
1. Scandinavian	Norway	(61-64)
	Sweden	(41, 42, 44, 62, 65-67)
2. Karelian	Finland	(68-73)
	Norway	(62, 63)
3. Baltic	Estonia	(74-79)
	Latvia	(80, 81)
4. Carpathian	Poland	(82-85)
	Romania	(9, 67, 78, 86)
	Serbia	(9)
	Slovakia	(67, 78, 87-90)
5. East Balkan	Bulgaria	(9, 88, 91-94)
	Serbia	(9)
	FYR Macedonia	(9, 95)
6. Dinaric-Pindus	Albania	(9, 95-101)
	Bosnia-Herzegovina	(9, 102)
	Croatia	(103-105)
	Greece	(9, 72, 87, 106-110)
	Kosovo	(9)
	FYR Macedonia	(9, 111)
	Montenegro	(9)
	Serbia	(9, 112, 113)
	Slovenia	(114-117)
7. Central Apennines	Italy	(43, 118, 119)
8. Alps	Austria	(27, 120)
	Italy	(72, 121, 122)
	Slovenia	(116, 117)
	Switzerland	(123)
9. Pyrenean	France	(87, 124-127)
	Spain	(87, 128, 129)
10. Cantabrian	Spain	(130-132)

Table S2. Brown bear population sizes and change. Literature is cited in Table S1 and further details are provided in (9). Recent estimates are for years 2010, 2011 or 2012 and methodologies may vary between countries. Some numbers may contain double count of border individuals. Past estimates refer to the lowest abundance during the 1950-1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled, < 0.3 means it has decreased by more than one third, “Return” indicates the species came back naturally after extinction and “Reintrod.” indicates the species came back through reintroduced animals. Countries may be labeled as “Reintrod.” if their sub-population originates from reintroduced animals in a neighboring country. “-“ indicates no data is available.

Population	Country	Recent estimate (individuals)	Past estimate (individuals)	Change factor
1. Scandinavian	Norway	105	15–41	> 3
	Sweden	3,300	400–600	> 5
	<i>Total</i>	3,400	410–640	> 5
2. Karelian	Finland	1,600–1,800	150	> 10
	Norway	46	9–26	> 2
	<i>Total</i>	1,700	160–180	> 10
3. Baltic	Estonia	700	100	> 5
	Latvia	10–15	Almost extinct	Return
	<i>Total</i>	710	100	> 5
4. Carpathian	Poland	80	10–14	> 5
	Romania	6,000	860	> 5
	Serbia	6	-	-
	Slovakia	800–1,100	300	> 3
	<i>Total</i>	7,200	-	-
5. East Balkan	Bulgaria	530–590	450	Stable
	Serbia	50	-	-
	FYR	-	-	-
	Macedonia	-	-	-
	<i>Total</i>	600	-	-
6. Dinaric-Pindus	Albania	180-200	-	-
	Bosnia-Herzegovina	550	400	> 1.3
	Croatia	1,000	400	> 2
	Greece	350–400	100	> 3
	Kosovo	-	-	-
	FYR	160–200	-	-

	Macedonia			
	Montenegro	270	-	-
	Serbia	50–70	-	-
	Slovenia	396–480	190	> 2
	<i>Total</i>	3,070	-	-
7. Central Apennines	Italy	37–52	40	Stable
8. Alps	Austria	5	Extinct	Return
	Italy	33–36 (Trentino) + 12 (Friuli)	8–10	Reintrod. (Trentino) + Return (Friuli)
	Slovenia	5–10	0–5	Return
	Switzerland	0–2	Extinct	Reintrod.
	<i>Total</i>	45–50	8–15	> 4
9. Pyrenean	France	22 (includes Spanish bears)	70 (includes Spanish bears)	< 0.3
	Spain	22–27 (include French bears)	70 (include French bears)	< 0.3
	<i>Total</i>	22–27	70	< 0.3
10. Cantabrian	Spain	195–210 (28 females with cubs of the year)	60	> 3
<i>Total</i>		17,000	-	-

Table S3. Range in km² occupied by brown bears and change. Literature is cited in Table S1 and further details are provided in (9). Our definition of range is not in the sense of the Article 17 of the 92/433/EEC Habitats Directive (no smoothing over gaps) but rather is representing occurrence or occupied cells in the EEA 10 x 10 km grid. Methodologies may vary between countries. Overlapping or border cells were only counted once. Past estimates refer to the lowest extend during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled, < 0.3 means it has decreased by more than one third. “-“ indicates no data is available.

Population	Permanent range	Sporadic range	Total range	Past range	Change factor
1. Scandinavian	169,100	298,600	467,700	95,600	> 4
2. Karelian	80,100	301,400	381,500	108,000	> 3
3. Baltic	20,800	29,600	50,400	12,400	> 4
4. Carpathian	99,200	23,400	122,600	72,600	> 1.5
5. East-Balkan	18,900	20,100	39,000	13,000	> 3
6. Dinaric-Pindus	78,700	35,400	114,100	71,100	> 1.5
7. Central Apennines	2,300	41,00	6,400	imprecise data	-
8. Alps	1,400	10,800	12,200	600	> 20
9. Pyrenean	7,900	5,000	12,900	imprecise data	-
10. Cantabrian	7,700		7,700	1,800	> 4
<i>Total</i>	<i>485,400</i>	<i>726,200</i>	<i>1,211,600</i>	-	-

Table S4. Brown bear population monitoring methods. Literature is cited in Table S1 and further details are provided in (9). All methods may not be used on the whole species distribution area. Abbreviations: CMR: Capture-Mark-Recapture, FCOY: count of Females with Cubs Of the Year.

Population	Country	Monitoring methods
1. Scandinavian	Norway	Genetic CMR, dead bears, damage reports
	Sweden	Genetic CMR, telemetry, dead bears, damage reports, bear observation index provided by moose hunters, density extrapolation
2. Karelian	Finland	Genetic CMR, FCOY
	Norway	Genetic CMR, dead bears, damage reports
3. Baltic	Estonia	FCOY, snow tracking, observations
	Latvia	Sum of hunting ground "counts "
4. Carpathian	Poland	Telemetry, questionnaires to state forest divisions & national parks
	Romania	Genetic CMR, telemetry, camera trapping, snow tracking, FCOY, sum of hunting ground "counts"
	Serbia	Genetic CMR, camera trapping, density extrapolation
	Slovakia	Genetic CMR, telemetry, camera trapping, snow tracking, sum of hunting ground "counts", expert opinion
5. East Balkan	Bulgaria	Genetic CMR, bear tracks, sum of hunting ground "counts", density extrapolation, expert opinion
	Serbia	Genetic CMR, camera trapping, density extrapolation, expert opinion
	FYR Macedonia	Genetic CMR, camera trapping, bear tracks, sum of hunting ground "counts"
6. Dinaric-Pindus	Albania	Camera trapping, bear tracks, expert opinion
	Bosnia-Herzegovina	Sum of hunting ground "counts "
	Croatia	Genetic CMR, sum of hunting ground "counts", density extrapolation, coordinated feeding site counts
	Greece	Genetic CMR, FCOY, camera trapping

	Kosovo	-
	The Former Yugoslav Republic of Macedonia	Camera trapping, bear tracks, sum of hunting ground "counts"
	Montenegro	-
	Serbia	Genetic CMR, camera trapping, density extrapolation, expert opinion
	Slovenia	Genetic CMR, harvest data, coordinated feeding site counts
7. Central Apennines	Italy	Genetic CMR
8. Alps	Austria	Genetics, bear signs (SCALP criteria C1 & C2)
	Italy	Genetic CMR, camera trapping
	Slovenia	Genetic CMR, coordinated feeding site counts
	Switzerland	Genetics, telemetry, bear signs
9. Pyrenean	France	Genetic CMR, FCOY, bear signs, camera trapping
	Spain	Genetic CMR, FCOY, bear signs, camera trapping
10. Cantabrian	Spain	Genetic CMR, FCOY

Table S5. Lynx population names, countries and literature references. Populations have been designated for the purpose of this analysis according to (39). Literature refers to actual abundance and distribution data, monitoring methods, historical abundance and distribution data. Population data do not cover Belarus, Russia and Ukraine.

Population	Country	References
1. Scandinavian	Norway	(133-136)
	Sweden	(137, 138)
2. Karelian	Finland	(73, 139-141)
3. Baltic	Estonia	(74, 75, 142)
	Latvia	(143, 144)
	Lithuania	(9, 145, 146)
	Poland	(134, 147-149)
4. Carpathian	Bulgaria	(9, 134, 150-153)
	Czech	(154-158)
	Hungary	(159, 160)
	Poland	(134, 147-149)
	Romania	(9, 134, 161)
	Serbia	(162)
	Slovakia	(9, 134, 156, 163)
5. Balkan	Albania	(9, 96, 98-101, 134, 164)
	FYR Macedonia	(9, 134, 164, 165)
	Serbia, Kosovo, Montenegro, Greece	(9, 112, 134, 164, 166-171)
6. Dinaric	Croatia	(9, 172)
	Bosnia-Herzegovina	(9, 173)
	Slovenia	(134, 174)
7. Bohemian-Bavarian	Austria	(175)
	Czech	(155, 176, 177)
	Germany	(176, 178, 179)
8. Alpine	Austria	(180, 181)
	France	(182, 183)
	Italy	(184)
	Slovenia	(134, 174, 182)
	Switzerland	(49-51, 185-187)

9. Jura	France	(188)
	Switzerland	(49, 185)
10. Vosges- Palatinian	France	(188)
	Germany	(179)
11. Harz Mountain	Germany	(179, 189)

Table S6. Lynx population sizes and change. Literature is cited in Table S5 and further details are provided in (9). Recent estimates are for years 2010, 2011 or 2012 and methodologies may vary between countries. Some numbers may contain double count of border individuals. Past estimates refer to the lowest abundance during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled, < 0.3 means it has decreased by more than one third, “Return” indicates the species came back naturally after extinction and “Reintrod.” indicates the species came back through reintroduced animals. Countries may be labeled as “Reintrod.” if their sub-population originates from reintroduced animals in a neighboring country. “-“ indicates no data is available.

Population	Country	Recent estimate (individuals)	Past estimate (individuals)	Change factor
1. Scandinavian	Norway	384–408 (65–69 family groups)	150	> 2
	Sweden	1,400–1,900 (277 family groups)	175	> 5
	<i>Total</i>	1,800–2,300	350–450	> 5
2. Karelian	Finland	2,430–2,610	Almost extinct	Return
3. Baltic	Estonia	790	115	> 5
	Latvia	600	Almost extinct	Return
	Lithuania	40–60	21	> 2
	Poland	96	50	> 1.5
	<i>Total</i>	1,600	190	> 5
4. Carpathian	Bulgaria	11	Extinct	Return
	Czech	11	0–4	> 5
	Hungary	1–3	Extinct	Return
	Poland	200	100	> 2
	Romania	1,200–1,500	500	> 2
	Serbia	50	-	-
	Slovakia	300–400	300–500	Stable
	<i>Total</i>	2,300–2,400	-	-
5. Balkan	Albania	5–10	40–50	< 0.2
	FYR Macedonia	23	120	< 0.2
	Serbia, Kosovo,	15–25	80	< 0.2

	Montenegro			
	<i>Total</i>	40–50	280	< 0.2
6. Dinaric	Croatia	50	Extinct	Reintrod.
	Bosnia-Herzegovina	70	Extinct	Reintrod.
	Slovenia	10–15	Extinct	Reintrod.
	<i>Total</i>	120–130	<i>Extinct</i>	<i>Reintrod.</i>
7. Bohemian-Bavarian	Austria	5–10	Extinct	Reintrod.
	Czech	30–45	Extinct	Reintrod.
	Germany	12	Extinct	Reintrod.
	<i>Total</i>	50	<i>Extinct</i>	<i>Reintrod.</i>
8. Alpine	Austria	3–5	Extinct	Reintrod.
	France	13	Extinct	Reintrod.
	Italy	10–15	Extinct	Reintrod.
	Slovenia	5–10	Extinct	Reintrod.
	Switzerland	96–107	Extinct	Reintrod.
	<i>Total</i>	130	<i>Extinct</i>	<i>Reintrod.</i>
9. Jura	France	76	Extinct	Reintrod.
	Switzerland	28–36	Extinct	Reintrod.
	<i>Total</i>	110	<i>Extinct</i>	<i>Reintrod.</i>
10. Vosges-Palatinian	France	19	Extinct	Reintrod.
	Germany	0	Extinct	Reintrod.
	<i>Total</i>	19	<i>Extinct</i>	<i>Reintrod.</i>
11. Harz Mountain	Germany	10	Extinct	Reintrod.
<i>Total</i>		9,000		

Table S7. Range in km² occupied by lynx and change. Literature is cited in Table S5 and further details are provided in (9). Our definition of range is not in the sense of the Article 17 of the 92/433/EEC Habitats Directive (no smoothing over gaps) but rather is representing occurrence or occupied cells in the EEA 10 x 10 km grid. Methodologies may vary between countries. Overlapping or border cells were only counted once. Past estimates refer to the lowest extend during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled, < 0.3 means it has been divided by more than one third, “Return” indicates the species came back naturally after extinction and “Reintrod.” indicates the species came back through reintroduced animals. “-“ indicates no data is available.

Population	Permanent range	Sporadic range	Total range	Past range	Change factor
1. Scandinavian	476,100	240,400	716,500	155,800	> 4
2. Karelian	92,000	253,800	345,800	17,700	> 10
3. Baltic	82,300	44,700	127,000	95,200	> 1.3
4. Carpathian	112,600	34,700	147,300	78,700	> 1.5
5. Balkan	4,500	14,100	18,600	18,600	Stable
6. Dinaric	20,200	9,800	30,000	0	Reintrod.
7. Bohemian-Bavarian	5,600	10,100	15,700	0	Reintrod.
8. Alpine	9,300	15,000	24,300	0	Reintrod.
9. Jura	9,400	8,400	17,800	0	Reintrod.
10. Vosges-Palatinian	1,400	4,600	5,600	0	Reintrod.
11. Harz Mountain	300	2,100	2,400	0	Reintrod.
<i>Total</i>	<i>813,400</i>	<i>632,800</i>	<i>1,446,200</i>	<i>366,000</i>	<i>>3</i>

Table S8. Lynx population monitoring methods. Literature is cited in Table S5 and further details are provided in (9). All methods may not be used on the whole species distribution area. Abbreviations: CMR: Capture-Mark-Recapture, SCALP: Status and Conservation of the Alpine Lynx Population (see (51, 52) and <http://www.kora.ch/en/proj/scalp>)

Population	Country	Monitoring methods
1. Scandinavian	Norway	Telemetry, camera trapping, snow tracking, harvest data, damage reports
	Sweden	Telemetry, camera trapping, snow tracking, harvest data, damage reports
2. Karelian	Finland	Telemetry, snow tracking
3. Baltic	Estonia	Telemetry, snow tracking, observations
	Latvia	Telemetry, harvest data, sum of hunting ground "count", expert opinion
	Lithuania	Snow tracking, sum of hunting ground "count", expert opinion
	Poland	Genetics, telemetry, snow tracking, lynx signs, expert opinion
4. Carpathian	Bulgaria	Camera trapping, snow tracking, questionnaires and follow up field investigations to confirm presence
	Czech	Genetics, telemetry, camera trapping CMR, snow tracking, sum of hunting ground "counts" through questionnaires
	Hungary	Camera trapping, questionnaires and follow up field investigations to confirm presence, expert opinion
	Poland	Genetics, telemetry, snow tracking, confirmed presence signs, expert opinion
	Romania	Genetics, telemetry, camera trapping, snow tracking, sum of hunting ground "counts"
	Serbia	Camera trapping
	Slovakia	Genetics, telemetry, camera trapping, snow tracking, sum of hunting ground "counts"
5. Balkan	Albania	Camera trapping, snow tracking, observations, questionnaires
	FYR	Genetics, telemetry, camera trapping,

	Macedonia	snow tracking, density extrapolation, lynx signs (SCALP criteria C1 & C2)
	Kosovo	Questionnaires
6. Dinaric	Croatia	Genetics, telemetry, camera trapping, snow tracking, dead lynx
	Bosnia-Herzegovina	Snow tracking, dead lynx
	Slovenia	Genetics, telemetry, lynx signs (SCALP methodology)
7. Bohemian-Bavarian	Austria	Camera trapping, lynx signs (SCALP criteria C1 & C2 and selected C3)
	Czech	Genetics, CMR camera trapping, snow tracking, sum of hunting ground "counts" through questionnaires every 2 years
	Germany	Telemetry, CMR camera trapping, snow tracking, lynx signs (SCALP criteria C1 & C2)
8. Alpine	Austria	Telemetry, camera trapping, lynx signs (SCALP criteria C1 & C2)
	France	CMR camera trapping, lynx signs (SCALP criteria C1 & C2 and selected C3)
	Italy	Telemetry, camera trapping, lynx signs (SCALP criteria C1 & C2)
	Slovenia	Genetics, lynx signs, snow tracking, expert opinion,
	Switzerland	Genetics, telemetry, CMR camera trapping, lynx signs (SCALP criteria C1 & C2)
9. Jura	France	CMR camera trapping, lynx signs (SCALP criteria C1 & C2 and selected C3)
	Switzerland	Genetics, telemetry, CMR camera trapping, lynx signs (SCALP criteria C1 & C2)
10. Vosges-Palatinian	France	CMR camera trapping, lynx signs (SCALP criteria C1 & C2 and selected C3)
	Germany	CMR camera trapping, lynx signs (SCALP criteria C1 & C2)
11. Harz Mountain	Germany	Telemetry, camera trapping

Table S9. Wolf population names, countries and literature references. Populations have been designated for the purpose of this analysis according to (39). Literature refers to actual abundance and distribution data, monitoring methods, historical abundance and distribution data.

Population	Country	References
1. Scandinavian	Sweden	(54-56, 190)
	Norway	(54-56, 191)
2. Karelian	Finland	(55, 56, 73, 192-197)
3. Baltic	Estonia	(74, 75, 198, 199)
	Latvia	(198, 200)
	Lithuania	(146, 198, 201, 202)
	Poland	(203, 204)
4. Central European Lowlands	Germany	(205, 206)
	Poland	(9, 203, 204)
5. Carpathian	Czech	(158, 207)
	Hungary	(208-210)
	Poland	(203, 204, 211)
	Romania	(9, 197)
	Slovakia	(197, 212-214)
6. Dinaric-Balkan	Albania	(9, 96-101, 215)
	Bosnia-Herzegovina	(9, 216, 217)
	Bulgaria	(9, 216, 218-220)
	Croatia	(216, 221-223)
	Greece	(197, 224-229)
	FYR Macedonia	(9, 216)
	Serbia	(9, 112, 216, 230, 231)
7. Italian peninsula	Slovenia	(232-234)
	Italy	(235-239)
8. Alpine	Austria	(9)
	France	(57)
	Italy	(58, 240)
	Switzerland	(185, 241)
9. NW Iberian	Spain	(59, 60, 242-245)
	Portugal	(246-249)

10. Sierra Morena	Spain	(59, 243-245)
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Table S10. Wolf population sizes and change. Literature is cited in Table S9 and further details are provided in (9). Recent estimates are for years 2010, 2011 or 2012 and methodologies may vary between countries. Some numbers may contain double count of border individuals. Past estimates refer to the lowest abundance during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled, < 0.3 means it has decreased by more than one third, “Return” indicates the species came back naturally after extinction. “-“ indicates no data is available.

Population	Country	Recent estimate (individuals)	Past estimate (individuals)	Change factor
1. Scandinavian	Sweden	230–300 (30 packs + 25 pairs, incl. border wolves)	Extinct	Return
	Norway	30 (3 packs + 2 pairs, exclud. border wolves)	Extinct	Return
	<i>Total</i>	260–330	<i>Extinct</i>	<i>Return</i>
2. Karelian	Finland	150–165	Almost extinct	Return
3. Baltic	Estonia	200–260	-	-
	Latvia	200–400	Almost extinct	Return
	Lithuania	300	34–56	> 5
	Poland	267–359 (67–77 packs)	11	> 28
	<i>Total</i>	870–1,400	-	-
4. Central European Lowlands	Germany	43 (14 packs + 3 pairs)	Extinct	Return
	Poland	100–110 (22 packs + 2 pairs)	Extinct	Return
	<i>Total</i>	150	<i>Extinct</i>	<i>Return</i>
5. Carpathian	Czech	1	Extinct	Return
	Hungary	1–5	Extinct	Return
	Poland	209–254 (47–51 packs)	45	> 5
	Romania	2,300–2,700	1550	> 1.5
	Slovakia	200–400	100–150	> 2
	<i>Total</i>	3,000	1700	> 1.5

	Albania	200–250	-	-
	Bosnia-Herzegovina	650	1000	< 0.7
	Bulgaria	700–800	100–150	> 5
	Croatia	168–219 (50 packs)	50	> 5
	Greece	700	500	> 1.4
	FYR Macedonia	466	267	> 1.5
	Serbia	750–850	500–600	> 1.4
	Slovenia	32–43	10–15	3
	<i>Total</i>	3,900	-	-
6. Dinaric-Balkan	Italy	600–800	100	> 5
7. Italian peninsula	Austria	2–8	Extinct	Return
	France	13 packs + 7 border ones	Extinct	Return
	Italy	12 packs + 7 border ones	Extinct	Return
	Switzerland	8	Extinct	Return
	<i>Total</i>	160 (32 packs)	Extinct	Return
8. Alpine	Spain	2,000	350–500	> 4
	Portugal	220–435	150–200	> 1.5
	<i>Total</i>	2,200–2,500	500–700	> 3
9. NW Iberian	Spain	6 (1 pack)	60 (10 packs)	< 0.1
10. Sierra Morena	<i>Total</i>	12,000	-	-

Table S11. Range in km² occupied by wolves and change. Literature is cited in Table S9 and further details are provided in (9). Our definition of range is not in the sense of the Article 17 of the 92/433/EEC Habitats Directive (no smoothing over gaps) but rather is representing occurrence or occupied cells in the EEA 10 x 10 km grid. Methodologies may vary between countries. Overlapping or border cells were only counted once. Past estimates refer to the lowest extend during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled, < 0.3 means it has decreased by more than one third, “Return” indicates the species came back naturally after extinction. “-“ indicates no data is available.

Population	Permanent range	Sporadic range	Total range	Past range	Change factor
1. Scandinavian	55,600	170,500	226,100	0	Return
2. Karelian	25,300	112,400	137,700	41,100	> 3
3. Baltic	94,200	49,200	143,400	42,800	> 3
4. Central European Lowlands	15,700	8,400	24,100	0	Return
5. Carpathian	144,200	27,000	171,200	59,900	> 2
6. Dinaric-Balkan	256,500	74,900	331,400	139,300	> 2
7. Italian peninsula	55,000	2,400	57,400	9,900	> 5
8. Alpine	33,200	26,800	60,000	0	Return
9. NW Iberian	116,600	3,700	120,300	69,200	> 1.5
10. Sierra Morena	800	0	800	12,900	< 0.1
<i>Total</i>	798,300	481,800	1,280,100	375,100	> 3

Table S12. Wolf population monitoring methods. Literature is cited in Table S9 and further details are provided in (9). All methods may not be used on the whole species distribution area. Abbreviations: CMR: Capture-Mark-Recapture.

Population	Country	Monitoring methods
1. Scandinavian	Sweden	Genetics, telemetry, snow tracking, dead wolves, damage reports
	Norway	Genetics, telemetry, snow tracking, dead wolves, damage reports
2. Karelian	Finland	Genetics, telemetry, snow tracking, howling
3. Baltic	Estonia	Genetics, snow tracking, howling observations, wolf signs
	Latvia	Harvest data, sum of hunting ground "counts", expert opinion
	Lithuania	Snow tracking, sum of hunting ground "count", expert opinion
	Poland (NE)	Genetics, telemetry, snow tracking, howling, wolf signs
4. Central European Lowlands	Germany	Genetics, telemetry, camera trapping, snow and sand tracking, wolf signs
	Poland (W)	Genetics, telemetry, snow tracking, howling, wolf signs
5. Carpathian	Czech	Snow tracking, wolf signs
	Hungary	Questionnaires and follow up field investigations to confirm presence, expert opinion
	Poland	Genetics, telemetry, snow tracking, howling, wolf signs
	Romania	Genetics, telemetry, camera trapping, snow tracking, howling, wolf signs, sum of hunting ground "counts"
	Slovakia	Genetics, camera trapping, snow tracking, sum of hunting ground "counts"
6. Dinaric-Balkan	Albania	Camera trapping, snow tracking, wolf signs, questionnaires, expert opinion
	Bosnia-Herzegovina	Snow tracking, wolf signs, damage reports, harvest data, expert opinion
	Bulgaria	Genetics, telemetry, snow tracking
	Croatia	Genetics, telemetry, camera trapping,

		snow tracking, howling, wolf signs, damage reports, expert opinion
	Greece	Genetics, telemetry, camera trapping, snow tracking, howling, wolf signs, damage reports, questionnaires, expert opinion
	The Former Yugoslav Republic of Macedonia	Sum of hunting ground "counts", expert opinion
	Serbia	-
	Slovenia	Genetic CMR, telemetry, snow tracking, howling
7. Italian peninsula	Italy	Genetics, telemetry, snow tracking, howling, density extrapolation, expert opinion
8. Alpine	France	Genetic CMR, snow tracking, howling, wolf signs
	Italy	Genetic CMR, snow tracking, howling, wolf signs
	Switzerland	Genetics, camera trapping, wolf signs
9. NW Iberian	Spain	Genetics, howling, wolf signs
	Portugal	Howling, wolf signs
10. Sierra Morena	Spain	Howling, wolf signs, damage reports

Table S13. Wolverine population names, countries and literature references.

Populations have been designated for the purpose of this analysis according to (39). Literature refers to actual abundance and distribution data, monitoring methods, historical abundance and distribution data.

Population	Country	Reference
1. Scandinavian	Norway	(250-254)
	Sweden	(251, 252, 255, 256)
2. Karelian	Finland	(73, 251, 253, 257, 258)

Table S14. Wolverine population size and change. Literature is cited in Table S13 and further details are provided in (9). Recent estimates are for years 2010, 2011 or 2012 and methodologies may vary between countries. Some numbers may contain double count of border individuals. Historical estimates refer to the lowest abundance during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled.

Population	Country	Recent estimate (individuals)	Past estimate (individuals)	Change factor
1. Scandinavian	Norway	339–431 (58 reproductions)	100–150	> 3
	Sweden	580–780 (118 reproductions)	60–100	> 5
	Total	919–1211	160–250	> 5
2. Karelian	Finland	165–175	20–30	> 5
<i>Total</i>		1084–1386	350–530	> 2

Table S15. Range in km² occupied by wolverines and change. Literature is cited in Table S13 and further details are provided in (9). Our definition of range is not in the sense of the Article 17 of the 92/433/EEC Habitats Directive (no smoothing over gaps) but rather is representing occurrence or occupied cells in the EEA 10 x 10 km grid. Methodologies may vary between countries. Overlapping or border cells were only counted once. Past estimates refer to the lowest extend during the 1950–1970s. Change factor indicates the rough multiplying factor from past to recent estimates, e.g. > 3 means the estimate has more than tripled.

Population	Permanent range	Sporadic range	Total range	Past range	Change factor
1. Scandinavian	220,200	163,500	283,700	93,900	> 3
2. Karelian	27,700	43,900	71,600	18,300	> 3
<i>Total</i>	<i>247,900</i>	<i>207,400</i>	<i>355,300</i>	<i>112,200</i>	<i>> 3</i>

Table S16. Wolverine population monitoring methods. Literature is cited in Table S15 and further details are provided in (9). All methods may not be used on the whole species distribution area. Abbreviations: CMR: Capture-Mark-Recapture.

Population	Country	Monitoring methods
1. Scandinavian	Norway	Snow tracking for natal den mapping, genetic CMR, dead wolverines, damage reports.
	Sweden	Snow tracking for natal den mapping, dead wolverines
2. Karelian	Finland	Snow tracking

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