Heterogeneity in the allocation of reintroduction efforts among terrestrial mammals in Europe

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Abstract

Reintroductions offer a powerful tool to reverse adverse anthropogenic impacts on biodiversity by restoring extirpated populations within the indigenous range of species. Reintroductions have become popular and have been increasingly used over the last decades. However, this species-centred conservation approach has been criticized for being taxonomically biased and for focusing on large and charismatic species. Studies investigating taxonomic biases in the allocation of reintroduction efforts at large scale generally consider taxonomic bias within and among higher taxa (e.g. vertebrates, plants), by comparing the number of reintroduced species within a taxon to its prevalence in nature. Here, we show that the bias is even more striking when accounting for the differences in the number of implemented programs among reintroduced species. We conducted a comprehensive search of the peer-reviewed and grey literature to inventory reintroduction programs of European terrestrial mammals. We identified 28 species that have been reintroduced at least one time. For each reintroduced mammal, we extensively searched two literature search engines and found 414 relevant publications, which described 375 distinguishable reintroduction programs implemented in Europe from the early 20th century to 2013. We used the number of implemented programs and the number of associated publications to investigate the distribution of reintroduction efforts among species. Our results show a substantial heterogeneity in the allocation of reintroduction efforts, with 68% of implemented reintroductions in Europe involving only three species: the beaver (*Castor fiber*), the Alpine ibex (*Capra ibex*) and the European bison (*Bison bonasus*).

Introduction

Biodiversity is under more severe threats than perceived when considering population declines and losses, rather than focusing only on species extinction (Ceballos, Ehrlich, & Dirzo, 2017). Effective conservation strategies are therefore required to reverse the dramatic shrinkage in species' geographical ranges, in order to support evolutionary trajectories in biological systems, as well as sustainable ecosystem functioning and services (Sarrazin & Lecomte, 2016). Reintroduction is the process of re-establishing a population in the indigenous range of a species where it has been extirpated (IUCN/SSC, 2013). Reintroduction is a popular restoration tool, as it moves towards the proactive return of locally extinct species into the wild if protective measures are not sufficient to ensure the return of the species. Reintroductions have been used for over a century, and the number of implemented programs, as well as the number of species involved have increased over the past decades (Seddon, Armstrong, & Maloney, 2007; Swan et al., 2016).

One interesting question in reintroduction biology is whether the accumulation of local reintroduction efforts have the potential to benefit to a wide array of threatened biodiversity at large taxonomic scale, which is not possible if most programs focus on, e.g., a few charismatic species. Using a database of reintroduction programs worldwide, yielding a total of 699 reintroduced species of plants and animals, Seddon, Soorae & Launay (2005) showed that vertebrate species were over-represented with respect to their prevalence in nature. Among them, reintroduced species were mostly mammals and birds, whereas fish were under-represented. More recently, similar biases within reintroduced mammals in Europe was uncovered, with a disproportionate list of reintroduced Carnivores and ungulates relative to their prevalence in the European assemblage of terrestrial mammals (Thévenin et al., 2018). These studies showed that reintroduction efforts are taxonomically and phylogenetically clustered within mammals, which is necessary to appreciate potential biases in reintroduction efforts. However, these studies focussed on the distinction between those species that have been reintroduced (at least once) vs. those that have not been reintroduced, without consideration for actual numbers of programs for each species. Here we provide a more in-depth look at the distribution of the number of implemented reintroduction programs per species. We focused on the list of 28 species of European terrestrial mammals that we identified as reintroduced at least once (Thévenin et al. 2018). For each species, we searched the ISI Web of Knowledge database and used Google Scholar search engine to identify reintroduction programs implemented over the past century. We described the heterogeneity in the implementation of population restoration programs and their reporting among European reintroduced mammals. The dataset we compiled allowed to explore the temporal and geographic distribution of reintroduction efforts in Europe.

Materials and Methods

Our primary objective here was to make an inventory of reintroduction "programs" aiming at re-establishing viable populations. Conceptually, we define a "population" based on the common biological meaning of the term i.e., a group of organisms of the same species occupying a particular space at a particular time and interacting more with each other than with individuals of the same species located at a distance they cross only through rare dispersal events (see Berryman, 2002, for a general discussion, and Robert et al., 2015, in the context of conservation translocations). This theoretical definition of a population is of course associated with practical difficulties in defining the boundaries of populations in the field, particularly for species with continuous distribution or where distribution data are missing. These difficulties are particularly important in our study regarding the aggregation (or separation) of reintroduction programs, and also in the case of metapopulations. We consider here that individual reintroduction programs are defined at the population level. In other words, each program aims to create a population, even when that population is part of an identified metapopulation. At the population organizational level, only reintroductions are considered (i.e. attempts to restore an extinct local population), although the program could be considered as a "reinforcement" at the metapopulation level. Intended reintroductions were not included (e.g., feasibility studies with no indication that individuals were released). We performed a comprehensive search (Swan et al., 2016) of the reintroduction and translocation-related literature to identify past and ongoing reintroduction programs implemented in the European subcontinent, including the western part of Russia and excluding Turkey. Using the list of 28 previously identified reintroduced species among the IUCN list of 202 native European terrestrial mammals (Thévenin et al., 2018), we performed independent queries for each species using the ISI Web of Science database, including all indexed peer reviewed literature. Because substantial information about translocation programs can be found in the grey literature, we also run each query on Google Scholar and searched for additional references in the first 50 records. We performed this search in the spring of 2016 and considered all published records available online up to May 1st, 2016. Our search terms were selected to maximize specificity at the expense of sensitivity, in order to focus on reintroductions and avoid publications relating to reinforcements of existing populations or mitigation translocations used to manage human-wildlife conflicts (Table 1). To account for potential taxonomic revisions over time and the fact that the species' name used by the authors at the time of publication may no longer correspond to the current name, the species search terms included both the Latin name and English common name along with all relevant synonyms available on the "Taxonomy" section of the Species Fact Sheet provided by the IUCN Red List website (available at www.iucnredlist.org). For example, the species search terms used for identifying translocations of Water voles (*Arvicola amphibius*) included the following terms: “European Water Vole” OR “Eurasian Water Vole” OR “Water Vole” OR “*Arvicola amphibius*” OR “*Arvicola terrestris*” OR “*Mus amphibius*”.

Table 1: List of the terms used to identify reintroduction programs for native terrestrial mammals in Europe

Category	Search Term
Species	Latin name OR synonym(s) OR Common name(s)
Translocation	reintroduc* OR re-introduc* OR translocat* OR re-establish* Or releas* OR relocat*
	AND
Motive	population* OR conserv* OR restorat*
	AND
Location	Europe*

*Terms were used in the ISI Web of Science database and Google Scholar search engine to identify documented reintroduction programs. *Indicates the use of a wildcard; for example, reintroduc* can refer to reintroduction OR reintroductions OR reintroduce OR reintroduces OR reintroduced OR reintroducing.*

We accurately screened each publication to determine which publications were relevant, that is, which described at least one program of translocation and release of individuals that we considered to be a reintroduction based on the intent and location of releases, i.e. the attempt to re-establish a free-ranging population in the former range of the species where it has been extirpated (IUCN/SSC, 2013). Reintroductions of mammals often involve game species (Griffith et al., 1989), and it was sometimes difficult to fully grasp whether the main purpose of the translocation would lean towards species exploitation rather than long-term conservation. Reintroductions of potential game species were included when they clearly aimed at restoring a viable population in the wild. Other cases where conservation did not seem to be the primary objective of releases were considered as restocking translocations and not integrated in our data (Supplementary Information, Table S1). Sometimes the full text was not accessible, but we included the publication if we could unambiguously extract all relevant and necessary information from the abstract. If a publication describing a reintroduction failed to provide the basic information (e.g., approximate year of first release) but explicitly mentioned other publications containing complementary information regarding the program, we extended our search to such cited literature. Some publications mentioned or described multiple reintroduction programs for a single species, usually reviewing the recovery of the focal species through time (e.g., Biebach & Keller, 2012). In such cases we considered the list of programs as described in these publications. Most of the publications we screened focused on a single species, with only seven publications mentioning or describing reintroduction programs for more than one species.

For each relevant publication, we extracted the year of publication, the species translocated, the approximated year of first release, and both the country and location of releases. The location of releases refers to the most precise sub-national geographic area encompassing the translocation site, and the level of precision varied substantially between publications (e.g., province, national park, nearest town). Some publications did not provide a precise date of first release, but rather a time interval, for which, in the absence of additional information, we deduced the year of first release as the middle of the given period (e.g., if individuals were "released in the 1970s", we considered the first year of release to be 1975). In some cases, multiple releases were clustered into a single reintroduction program if we deemed the different release events to contribute to the same population unit, based on the location of releases and expected home range of the species.

Results

Our searches on Web of Science yielded 1665 unique references, and we found 318 relevant references that described reintroduction programs precisely enough (year of first release, country and location of release site). We found 96 additional relevant references through our search on Google Scholar, or by extending our search to the cited references of some articles. These 414 publications, published between 1965 and March 2016, described 375 distinguishable reintroduction programs implemented between 1910 and 2013. The number of relevant publications increased over the past 30 years (Fig. 1). Reintroductions programs were implemented in 28 European countries, and most of these programs were undertaken in Switzerland (61), France (41), the United Kingdom (41) and Poland (36) (Fig. 2).

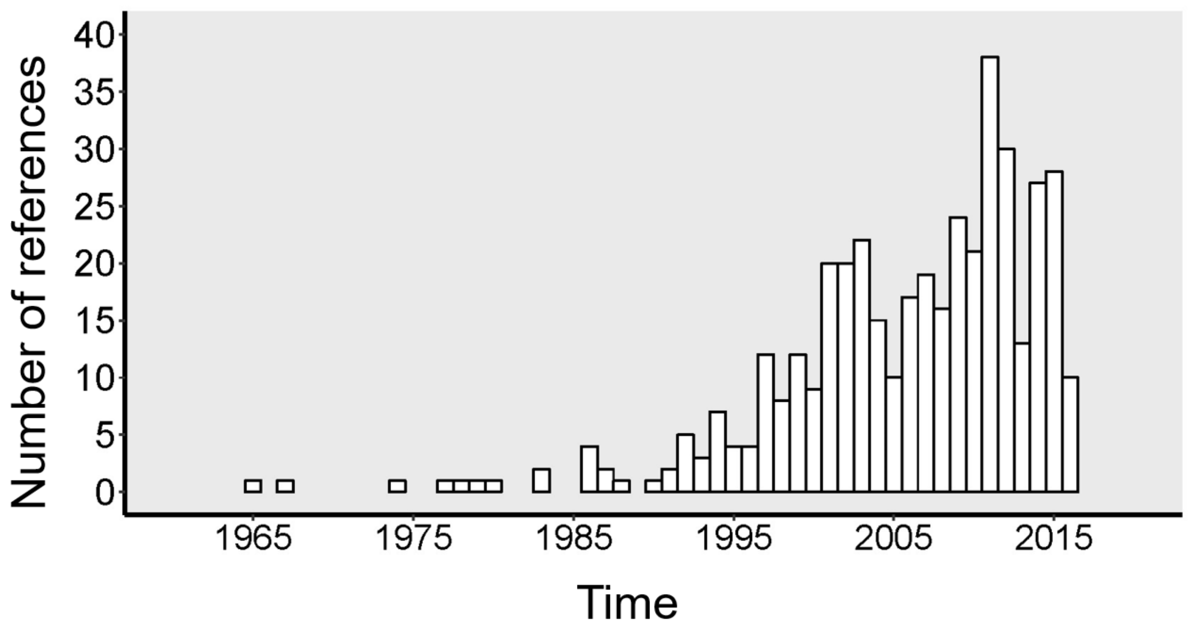

Fig. 1: Temporal distribution of the 414 relevant publications used to describe reintroduction programs for native European terrestrial mammals. The number of references in 2016 only accounts for publications between January and March.

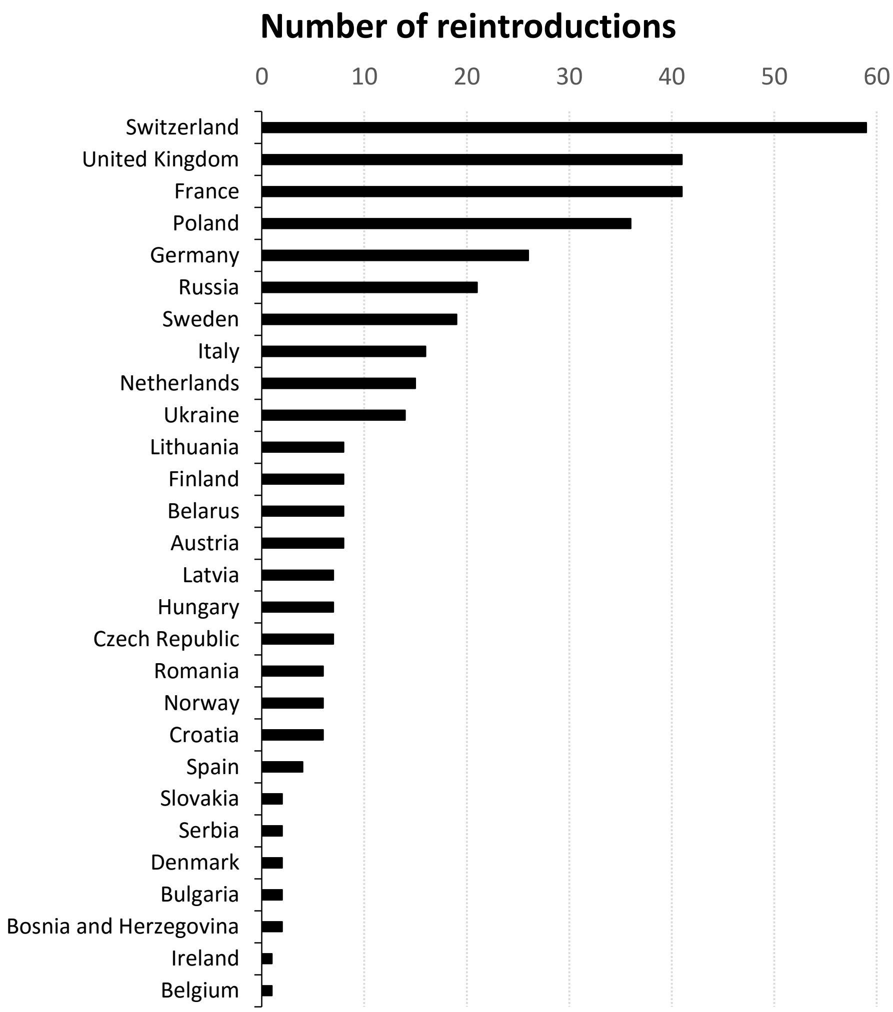

Fig. 2: Number of reintroduction programs by countries in the European subcontinent.

The allocation of reintroduction efforts per species was highly heterogeneous, with the number of programs ranging from only one reintroduction up to 164 (Fig. 3). Only six out of 28 species were involved in more than ten reintroduction attempts, and the median number of reintroduction programs per species was three. The beaver was the most reintroduced mammal in Europe and has been involved in more than 40% of all the reintroduction attempts we identified, followed by the Alpine ibex (54 programs, 14%) and the European bison (39 programs, 10%). The reporting effort per species was evaluated by considering the ratio of the number of publications over the number of programs for each species. Low values of this ratio indicate that relatively few publications described numerous reintroduction programs. This was the case for the 5 most reintroduced species in our dataset (*Castor fiber*, *Capra ibex*, *Bison bonasus*, *Muscardinus avellanarius*, *Arvicola amphibius*), with the lowest ratio being the Alpine ibex with 54 reintroduction attempts described using only 15 publications (ratio = 0.28). In contrast, some species have generated a substantial amount of publications relative to the number of releases, as exemplified with 5 reintroduction programs of brown bears (*Ursus arctos*) being described in 27 publications (ratio = 5.4). At higher taxonomic level, the distribution of reintroduction programs and associated references within the different orders of terrestrial mammals of Europe is significantly different from that expected on the basis of the number of described species in each order ($X^2 = 506.68$, *d.f.* = 5, $P < 0.001$; $X^2 = 379{,}55$, *d.f.* = 5, $P < 0.001$; respectively) (Fig. 4). Closer examination of taxa reveals that Artiodactyla is clearly over-represented both in terms of implemented programs and associated publications (Pearson residuals of +18.77 and +9.91, respectively). On the other hand, the Carnivora order shows a contrasting pattern: Carnivores are slightly under-represented when considering the number of implemented programs (Pearson residuals of -2.32) but are over-represented when considering the associated publications (Pearson residuals of +11,82) (Fig. 4).

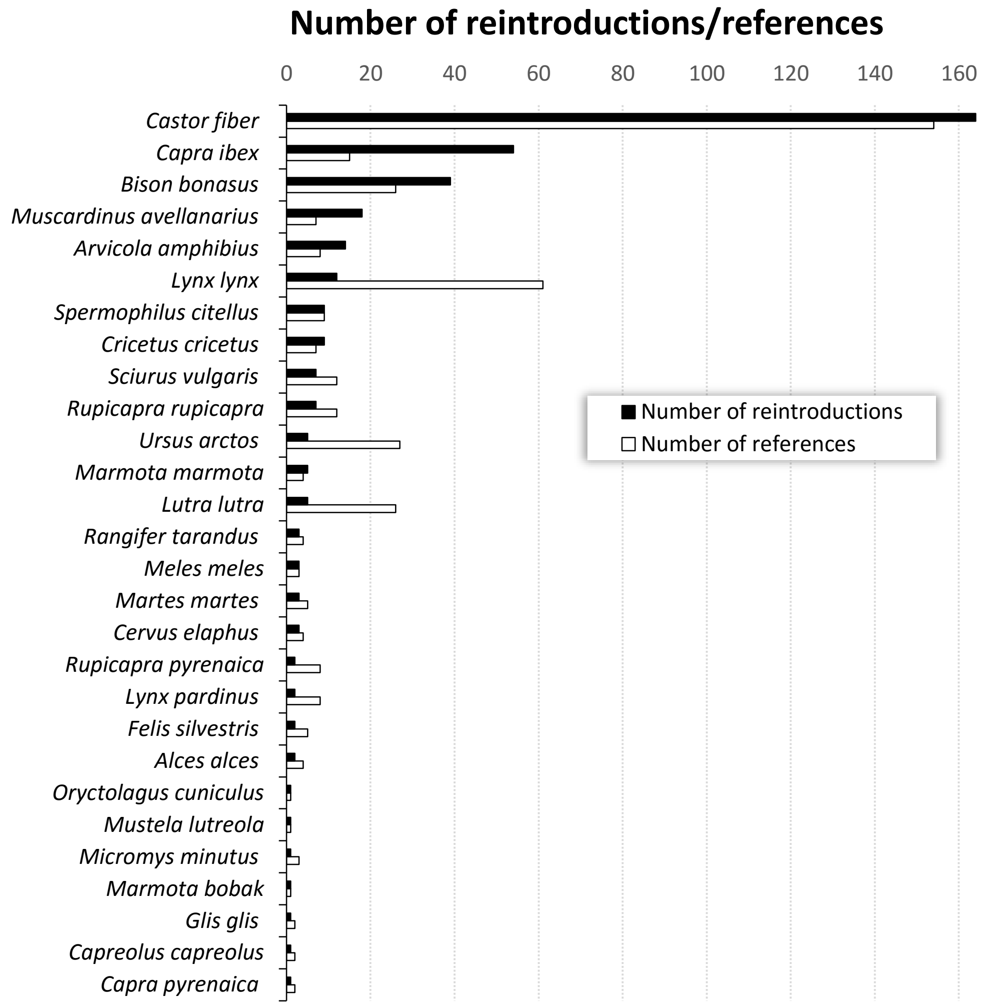

Fig. 3: Number of reintroduction programs (black bars) and associated references (white bars) for the 28 terrestrial mammals reintroduced in Europe. Because some publications described reintroductions for different species, the total number of references here is larger than the number of unique references.

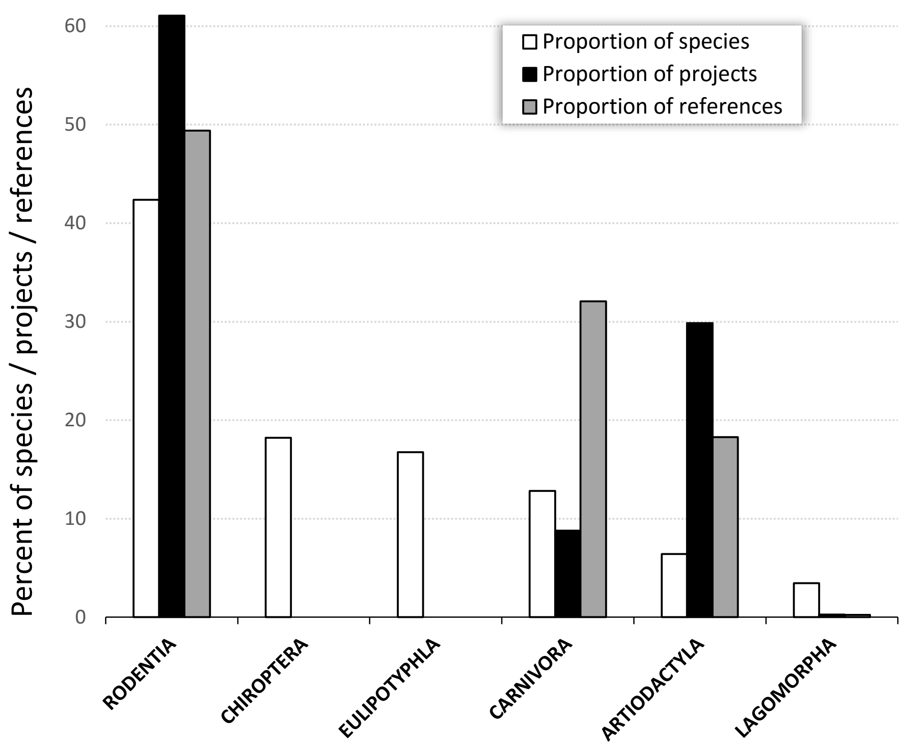

Fig. 4: Proportion of species out of the 202 European terrestrial mammals per taxonomic order (white bars) compared to the proportion of reintroduction programs (black bars) and the proportion of associated references (grey bars).

The two oldest programs in our data are the reintroduction of the red squirrel (*Sciurus vulgaris*) into Epping Forest, Ireland, in 1910 (MacKinnon, 1978), and the reintroduction of the Alpine ibex in Graue Hoerner, Switzerland, which started in 1911 (Stüwe & Nievergelt, 1991; Biebach & Keller, 2012). The number of reintroduction programs has increased throughout the time period (Fig. 5a), and the apparent diminution in the number of reintroduction programs from 2006 onward can be attributed to a time lag between releases, data collection and any associated publication (Fazey, Fischer, & Lindenmayer, 2005; Swan et al., 2016). For most of the first half of the 20th century (up to the late 1950s), reintroductions of terrestrial mammals in Europe mainly involved beavers or Alpine ibex (51 and 28 programs respectively, out of 86). The other species reintroduced in this time period were the above mentioned red squirrel, the elk (*Alces alces*; Schönfeld, 2009; Świsłocka et al., 2013), the brown bear (Buchalczyk, 1980) and the reindeer (*Rangifer tarandus*; Røed et al., 2014). When considering the three mostly reintroduced species in our data, we can see that beavers have benefited from a consistent and continuous reintroduction effort throughout the entire time period considered (Fig. 5b). Reintroductions of Alpine ibex mostly occurred in the first half of the time period (the last release in our dataset occurred in 1995), with a cluster of programs around the centre of the study period (1950-1970) (Fig. 5c). Most of the restoration of free-ranging populations of the European bison took place in the past 60 years (Krasińska & Krasiński, 2013) (Fig. 5d).

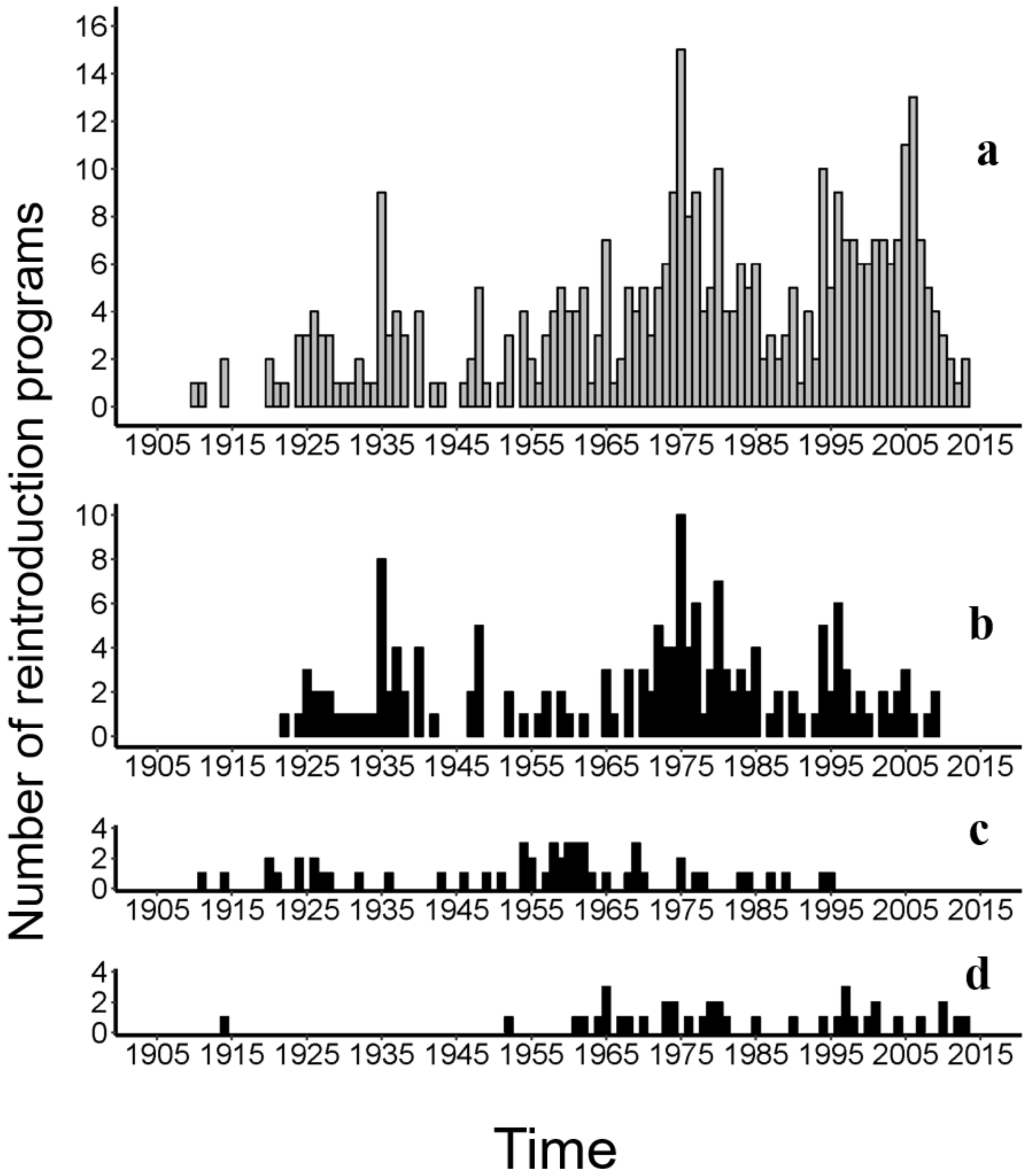

Fig. 5: (a) Temporal distribution of reintroduction programs of 28 species of native terrestrial mammals in Europe (n = 375); (b) reintroduction programs of beavers (n = 164); (c) reintroduction programs of Alpine ibex (n = 54) and (d) reintroduction programs of European bison (n = 39). The distribution of reintroduction programs is based on approximated date of first release.

Discussion

Previous studies have shown that the allocation of reintroduction efforts is taxonomically (and phylogenetically) clustered by focussing on the distinction between those species that have been reintroduced (at least once) vs. those that have not been reintroduced (Seddon et al. 2005, Thévenin et al. 2018). Here we show that this heterogeneity is more striking when accounting for the number of implemented programs among reintroduced species.

The most reintroduced species in our dataset are the beaver, the Alpine ibex and the European bison, for which the main cause of population extirpation was overhunting (Stüwe & Nievergelt, 1991; Pucek et al., 2004). Of all reintroduced mammals, the remarkable recovery of European beavers presumably benefited from widespread reintroductions. At the end of the 19th century, the species was reduced to about 1200 individuals scattered in 8 small relict populations and would have been listed then as critically endangered (Halley, Rosell, & Saveljev, 2012). Reintroductions started in 1922 in Sweden and were later implemented in 20 other European countries. Early successes with remarkably little planning or monitoring confirmed the beaver as a reliable candidate for reintroductions, and may have triggered a self-reinforcing feedback for more implementations of programs over the years (Halley & Rosell, 2002). Such self-reinforcing feedbacks where early reintroduction success may foster the implementation of new programs for some species may further contribute to the heterogeneity of restoration efforts among species. Incentives for restoring viable populations of beavers were initially associated to fur-harvesting and future economic gains, and later reintroductions became more motivated by ecosystem management reasons. The beaver is considered a key-stone species, which substantially impacts the structure and dynamics of aquatic ecosystems at the landscape level. Beaver's dams influences the hydrology of surrounding areas, thus altering nutrient cycles and subsequently modifies the structure of invertebrate and plant communities

(Macdonald et al., 1995). Such prominent and well-documented functional role of the species in its recipient ecosystem may have played a role in the disproportionate, large scale effort that was invested into its restoration.

Considering the number of implemented programs allows to reinterpret reintroduction biases between mammalian orders in Europe. A previous study has shown that, among mammals, Carnivores and Ungulates are over-represented in reintroduction efforts at a worldwide scale (Seddon, Soorae, & Launay, 2005). More than half of the reintroduced species of mammals in Europe are members of the Artiodactyla or the Carnivora orders, although these orders represent less than 20% of species in the European assemblage of native mammals (Thévenin et al. 2018). However, when accounting for the number of implemented programs, the pattern is clearly maintained for ungulates (30% of implemented programs), but Carnivores are no longer over-represented (8% of implemented programs). One interesting finding of this study is that reintroduced Carnivores seem to benefit from a higher reporting effort.

Our results show that some reintroduced species are relatively more reported in the literature. The species with the most imbalanced ratio of the number of publications over the number of associated publications are the Eurasian lynx (*Lynx lynx*), the brown bear and the otter (*Lutra lutra*). Predators are charismatic species that are often employed in conservation because they can easily gather public interest (i.e., “flagship species”, *sensu* Simberloff 1998), and such societal preferences may influence the choice of study species and lead to more publications. Even though large carnivores are now recovering throughout Europe thanks to favourable legislation and increases in prey availability (Chapron et al., 2014), the reintegration of such large predators comes with many challenges that may require making adjustments to the practices of some sectors like livestock farming, forestry or hunting (Breitenmoser et al., 2010; Boitani & Linnell, 2015). Restoring populations of large predators where they have been extirpated constitutes a major challenge if adaptations to coexistence have been lost and if husbandry practices have evolved. Reintroductions of top predators can have economic costs (e.g., predation on livestock) and trigger social conflicts that need to be carefully addressed and managed (Stahl et al., 2001), which is likely to generate additional research and publications.

Our search of the literature is certainly not exhaustive, but we believe that our data provide a good and representative proxy of the allocation of reintroduction efforts for European terrestrial mammals. Publication biases in conservation and reintroduction research have been documented, and show that some species receive disproportionate attention, and that successful translocations are more likely to be published than failed ones or those with uncertain outcomes (Fischer & Lindenmayer, 2000; Clark & May, 2002; Fazey, Fischer, & Lindenmayer, 2005; Bajomi et al., 2010; Miller, Bell, & Germano, 2014; Troudet et al., 2017). While our results provide a highly indicative description of reintroduction efforts for native European terrestrial mammals, we acknowledge that our data on reintroduction programs partly reflect publication effort and are likely to underestimate the number of programs implemented throughout Europe.

Another issue lies in the access to past publications, and how terminology evolved over the years. Some documentation of reintroduction attempts implemented several decades ago may have yet to be digitalized and indexed, and programs that have been recently implemented might not have yet been described in the literature. Additionally, reporting of reintroduction efforts at a continental scale is challenged by gaps and heterogeneity in the collection and compilation of information related to restoration attempts. First, language may greatly influence the spatial distribution of our European data. We only considered sources written in English, and we suspect that we might have missed a substantial amount of information written in the native language of the reintroduction team. For example our search yielded 4 reintroduction programs in Spain over the last century, while Perez et al. (2012), who conducted an extensive review of translocation programs in Spain, taking into account Spanish language documentation, found 9 translocation programs implemented from 1996 onwards. Studies have shown that the availability of information on biodiversity is unevenly distributed around the world (Boakes et al., 2010), and that data availability is positively associated with country wealth and the proportion of English speakers (Amano & Sutherland, 2013). The high number of reintroductions found in the United Kingdom can also be explained by insularity, as species will have lower probabilities of natural recolonization after extinction, so that reintroduction becomes a valuable conservation option. The spatial distribution of our data is also greatly influenced by previous compilations and reviews of reintroduction programs in some areas. For example, 48 out of the 59 reintroductions identified in Switzerland involved the Alpine ibex, and 40 of these were mentioned in Biebach & Keller (2012). Similarly, 23 out of the 36 reintroduction programs we identified in Poland involved the beaver, which were all mentioned in one study on the expansion of the species in Europe by Kasperczyk (1987). Another source of variability in the spatial distribution of mammal reintroductions in Europe could be the list of nationally extinct mammals in European countries. Such conservation priorities at the national scale could further shape the distribution of reintroduction efforts at the continental scale.

In this study we used the number of implemented programs and the number of associated publications to estimate the reintroduction effort per species. This is only one way to assess how efforts are distributed in population restoration programs, and further studies are needed to explore other aspects such as the financial costs of programs, information on release strategies (number of individuals and number of release events), or how much effort was invested to insure habitat quality before release.

Over the past 30 years, the development of reintroduction biology has advocated for an improvement of reintroduction practice and implementation. Managers need to collect and use all available information to improve reintroduction design and benefit from knowledge accumulated through past attempts to restore populations (Sarrazin & Barbault, 1996; Ewen &

Armstrong, 2007; Armstrong & Seddon, 2008; IUCN/SSC, 2013). One important challenge is therefore to enhance the documentation and transmission of knowledge from past reintroduction programs. Some species, or groups of species (e.g. Carnivores) of mammals have benefited from reviewing efforts describing and inventorying reintroduction programs in Europe (Stüwe & Nievergelt, 1991; Halley & Rosell, 2002; Clark, Huber, & Servheen, 2002; Krasińska & Krasiński, 2013). Our data constitute a core contribution to the development of a webdatabase inventorying conservation translocation programs in Europe and the Mediterranean basin which will promote standardization in reintroduction reporting to improve their adaptive management (TRANSLOC webdatabase program, http://translocations.in2p3.fr/).

The reintroduction of wild mammals and particularly ungulates often emerges as a cornerstone in rewilding initiatives (Pettorelli et al., 2018; Pettorelli, Durant, & du Toit, 2019), especially in heavily anthropized landscapes such as Europe (Pedersen et al., 2019). In the rewilding framework, motivations for conservation translocations shift from species-centred actions towards the restoration of ecological and evolutionary processes at the ecosystem level, e.g., through trophic rewilding (Svenning et al., 2016; Bakker & Svenning, 2018; Perino et al., 2019). While further advances in the definition of rewilding and its distinction from ecological restoration are needed (Derham, 2019; Hayward, Jachowski, et al., 2019; Hayward, Scanlon, et al., 2019), the evaluation of past reintroduction efforts and understanding of their outcomes will necessarily benefit to any future program aiming at restoring wildness, i.e. functional and evolutionary potential in previously altered ecosystems.

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