Reintroductions of birds and mammals involve evolutionarily distinct species at the regional scale

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Reintroductions offer a powerful tool for reversing the effects of species extirpation and have been increasingly used over recent decades. However, this species-centered conservation approach has been criticized for its strong biases toward charismatic birds and mammals. Here, we investigated whether reintroduced species can be representative of the phylogenetic diversity within these two groups at a continental scale (i.e., Europe, North and Central America). Using null models, we found that reintroduced birds and mammals of the two subcontinents tend to be more evolutionarily distinct than expected by chance, despite strong taxonomic biases leading to low values of phylogenetic diversity. While evolutionary considerations are unlikely to have explicitly driven the allocation of reintroduction efforts, our results illustrate an interest of reintroduction practitioners toward species with fewer close relatives. We discuss how this phylogenetic framework allows us to investigate the contribution of reintroductions to the conservation of biodiversity at multiple geographic scales. We argue that because reintroductions rely on a parochial approach of conservation, it is important to first understand how the motivations and constraints at stake at a local context can induce phylogenetic biases before trying to assess the relevance of the allocation of reintroduction efforts at larger scales.

conservation translocations | conservation priorities | phylogenetic diversity | evolutionary isolation

When looking at population declines and losses rather than focusing only on species extinctions, Earth's biological diversity is under more severe threats than initially perceived (1). Therefore, effective conservation actions are required to sustain evolutionary trajectories in biological systems and to ensure ecosystem functioning and services (2). In this context, population restoration offers a tool to mitigate or reverse the consequences of local population extinctions; thus, population restoration promotes species persistence and counters the dramatic shrinkage in a species' geographical range (3).

Conservation translocations are human-mediated movements and releases of organisms, where the primary objective is to yield a measurable conservation benefit (4). Reintroductions are part of the conservation translocation spectrum, and reintroductions aim to reestablish a population in the species' indigenous range following local extinction or extirpation. Reintroductions have been used for over a century, and the number of programs, as well as the number of targeted species, have increased over recent decades (3, 5, 6). Except for some rare projects included in ecosystem restoration (7), reintroductions are primarily case-by-case initiatives that are locally designed population-centered conservation approaches. By definition, reintroductions follow the local extinction of a population, but they do not necessarily involve globally threatened species (8). In fact, reintroduction implementations are usually driven by national conservation targets, the ability to garner public and political support, or the technical feasibility of translocation releases. All of these factors are non-neutral with respect to taxonomy, with studies showing that mammals and birds are overrepresented in reintroduction

programs (5, 8). Reintroductions offer a powerful conservation tool. However, the fact that conservation goals are being set at the local scale should not hamper their ability to contribute to the conservation of biodiversity at large scales. If a bias toward birds and mammals is likely to persist, the focus of reintroductions should be on, when possible and with respect to national priority targets, species that are the most likely to contribute to the persistence of the diversity of the Tree of Life (9).

With scarce resources available for conservation, the objective prioritization among taxa and regions is required to maximize conservation returns (10, 11). Since the 1990s, scientists have promoted the incorporation of information on shared and nonshared evolutionary history between species into conservation prioritization. Based on the assumption that not all species contribute equally to biodiversity, additional value should be granted to evolutionarily distinct species, that is, those that lack close relatives, because the loss of a species in an old clade would result in a greater loss of biodiversity (9, 12). Based on the assumption that closely related taxa are more likely to share similar features, conservation strategies that aim to preserve high levels of evolutionary diversity should capture the value of biodiversity as variation (13) and potentially provide unanticipated benefits in the future (14–17). Some studies suggest that the rate of loss of evolutionary information could even be much higher than the rate of species loss, as the extinction threat is not randomly distributed in phylogeny (18). Thus, the consideration of evolutionary history in conservation decision making is a way to set relevant and objective conservation goals while also using easily communicable metrics, such

Significance

There are general acknowledgements that Earth's sixth mass extinction event is more severe than perceived when looking at population extirpations (rather than focusing only on species extinctions) and that species extinctions are associated with the rapid loss of evolutionary history. In this study, we investigate how population reintroductions, a major conservation tool used to reverse population extirpations, can contribute to the preservation of evolutionary diversity within birds and mammals. Using data on reintroductions of terrestrial birds and mammals in Europe and North America, we show that, despite strong taxonomic biases leading to a poor representativeness of the regional phylogenetic diversity, reintroduction practitioners seem to have focused on highly evolutionarily distinct species.
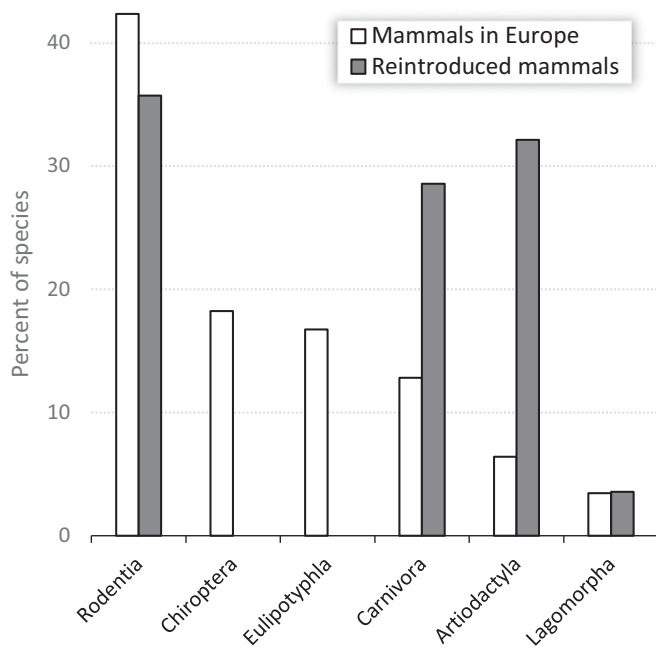
Fig. 1. Taxonomic distribution of reintroduced species within the different orders of the terrestrial mammals of Europe. Unshaded bars are the proportions of mammals out of the 202 species of Europe, and shaded bars are the proportions of mammals out of the 28 reintroduced species.

as the duration of species' evolutionary histories in terms of millions of years of evolution (19).

Methodological developments and the increasing amount of phylogenetic data available should foster the implementation of conservation projects based on evolutionary considerations (20–23). However, it also remains necessary to assess whether current management strategies are relevant to the conservation of evolutionary diversity. While gap analyses have examined the efficiency of current protected area networks on the protection of evolutionary diversity (24–26), the contribution of species-centered conservation measures [for example, translocations (3)] on the preservation of broad-scale evolutionary diversity is largely unknown.

Here, we investigated how the allocation of reintroduction efforts could contribute to biodiversity conservation at a continental scale, focusing on the phylogenetic dimension of biodiversity rather than on taxonomy. We focused on reintroduced terrestrial birds and mammals in Europe as well as in North and Central America (including Mexico and the Caribbean, but hereafter called North America) (*Materials and Methods*). We investigated the phylogenetic richness (i.e., quantity of phylogenetic differences) (27) expected for our focal subsets of reintroduced species (e.g., reintroduced European mammals) given the regional pool of species. First, we calculated the phylogenetic diversity (PD) (14) of each subset of reintroduced species, that is, their total amount of independent evolutionary history, to assess whether a focal subset of reintroduced species is representative of the regional phylogenetic diversity. Second, we quantified the evolutionary isolation of reintroduced species using the evolutionary distinctiveness (ED) index (20), which estimates the conservation value of each individual species based on its unique evolutionary history. We constructed null models to test the deviation of our two metrics from the value expected when species were randomly drawn in the associated regional phylogeny. Reintroduced species are not expected to collectively contribute to high PD because they are taxonomically clumped, but they might be more evolutionarily distinct than species drawn

at random if they come from less diverse clades (8). While our results confirmed these general expectations on PD, they indicated that the distribution of ED scores for reintroduced species vary according to the region or group considered. Overall, our work shows that the selection of species for reintroduction, which is mostly driven by conservation needs at local scales, either contrasts or converges with broad-scale, evolutionary-based conservation priorities depending on the metric being considered.

Results and Discussion

Evolutionary Diversity and Reintroductions. Twenty-eight mammalian species have been reintroduced at least once in Europe (i.e., 14% of the 202 terrestrial mammalian species), and these species are distributed among four orders: 10 rodents, 9 ungulates, 8 carnivores, and 1 lagomorph (Fig. 1). This taxonomic pattern is consistent with the results of North America (28), with the only difference being the reintroduction of two primates (*Alouatta pigra* and *Ateles geoffroyi*) in Central America. More than 50% of reintroduced mammals on both subcontinents are members of the orders Carnivora or Artiodactyla (Fig. 2). Thirty-seven bird species have been reintroduced at least once in Europe (i.e., 10% of the 378 terrestrial breeding bird species). The order Accipitriformes includes the highest number of reintroduced species of birds in Europe, followed by the order Galliformes (Fig. 3). We can see differences in the taxonomic distribution of reintroduced bird species between the two subcontinents, with the order Passeriformes accounting for 25% of the reintroduced birds in North America (Fig. 4); in contrast, Passeriformes account for only 1% of the reintroduced birds in Europe. Our results are consistent with previous studies showing that reintroduction efforts are strongly taxonomically biased within birds and mammals (8). In both regions, avian and mammalian reintroductions seem to favor large charismatic species (e.g., *Bison bonasus*, *Lynx pardinus*, *Gypaetus barbatus*), which easily garner
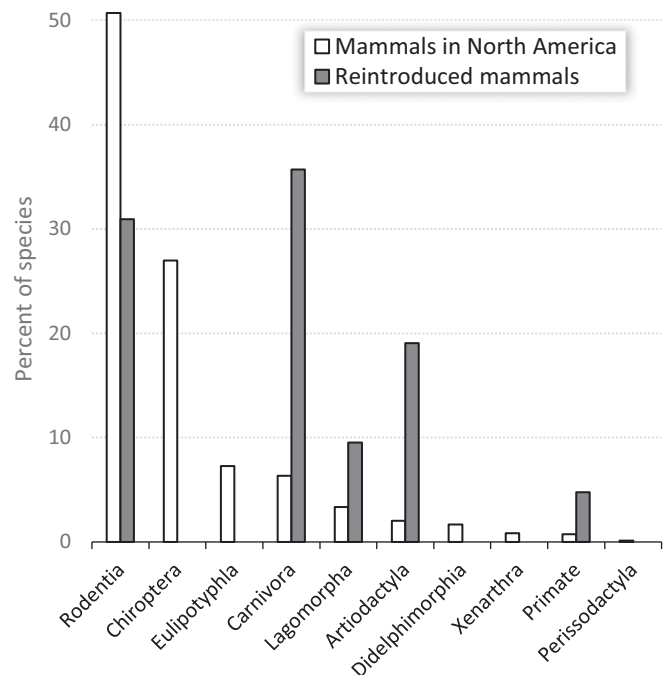

Fig. 2. Taxonomic distribution of reintroduced species within the different orders of the terrestrial mammals in North America (including Mexico, Central America, and the Caribbean). Unshaded bars are proportions of mammals out of the 838 species of North America, and shaded bars are the proportions of mammals out of the 42 reintroduced species.
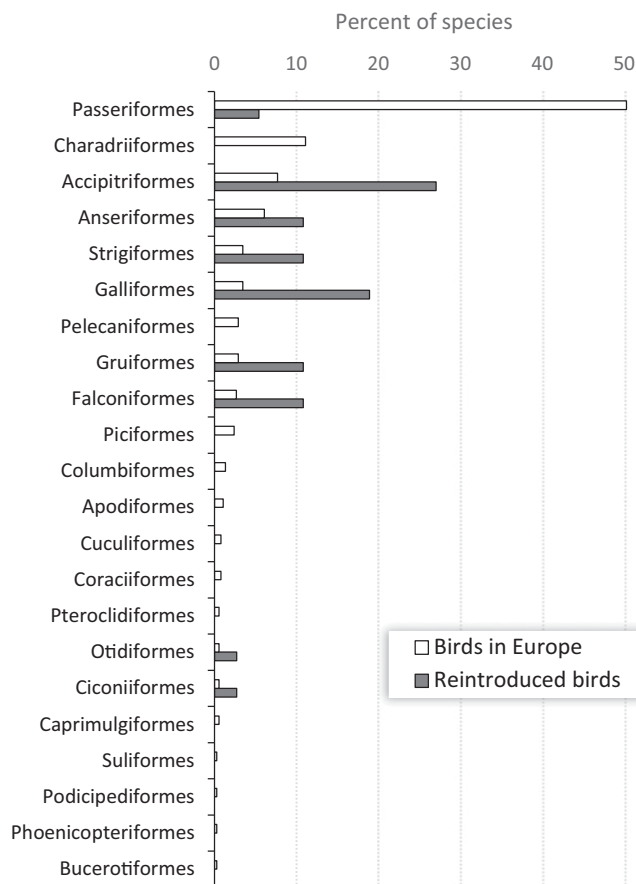
Thévenin et al.

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Percent of species

Fig. 3. Taxonomic distribution of reintroduced species within the different orders of the terrestrial birds of Europe. Unshaded bars are proportions of birds out of the 378 species of Europe, and shaded bars are the proportions of birds out of the 37 reintroduced species.

public support and funds for conservation, or exploited species (e.g., *Cervus elaphus*, *Capra ibex*, *Tetrao urogallus*), for which overharvesting could have led to local extinction.

Because of this taxonomic clustering in the allocation of reintroduction efforts, reintroduced birds and mammals in Europe and North America are poorly representative of the associated regional phylogenetic diversity. The PD measured for reintroduced mammals in North America is significantly lower than expected by chance (PD$_{reint}$ = 1,387.4 My; μ = 1,747.61 My; SD = 145.36; P value = 0.015) (Table 1), and the three remaining subsets of reintroduced species (i.e., European mammals, North American birds, and European birds) showed PD values lower than random expectations but did not significantly depart from our null model (i.e., associated P values ranged from 0.063 to 0.114) (Table 1). Low PD values observed for reintroduction target species might be caused by shared causes of extirpation, at least for mammals. Within mammals, extinction threats caused by hunting pressure are more strongly phylogenetically clumped than threats caused by habitat loss or invasive species (29). Reintroduction feasibility requires the identification and eradication of past threats and causes of extirpation (4); thus, the possibility of both identification and eradication of these threats may affect the selection of reintroduction candidate species. Overexploitation is likely to be the easiest threat to identify in the past extinction of vertebrates, and it is also likely to be easier to mitigate through strict protection and hunting regulations than the control of invasive species or the restoration of degraded habitat.

The concept of evolutionary distinctiveness appears only once in the International Union for Conservation of Nature (IUCN) *Guidelines for Reintroductions* (4). Managers undertaking reintroductions face multiple decisions, which can rely on competing objectives and uncertainty (30). Therefore, evolutionary considerations are not expected to ultimately influence the allocation of reintroduction efforts. However, our results show that there is a significant trend in the reintroduction of mammals and birds toward species with few close relative taxa at the continental scale. When considering the median ED score of reintroduced species, we found that reintroduced mammals in Europe and North America are more evolutionarily distinct than expected by chance, as the median ED is significantly higher than the random expected value (median ED$_{reint}$ = 20.84 My and 13.46 My; P value = 0.018 and P value < 0.001, respectively) (Table 2). In Europe, the median ED score of reintroduced bird species is higher than expected by chance (median ED$_{reint}$ = 19.81 My; P value = 0.047), while the median ED of reintroduced birds in North America is not significantly different from the random expected value (median ED$_{reint}$ = 8.76 My; P value = 0.99) (Table 2). Reintroduced birds with the highest ED value tend to be large-bodied species from less diverse clades (Accipitriformes, Strigiformes, Gruiformes) in both subcontinents. Because ED

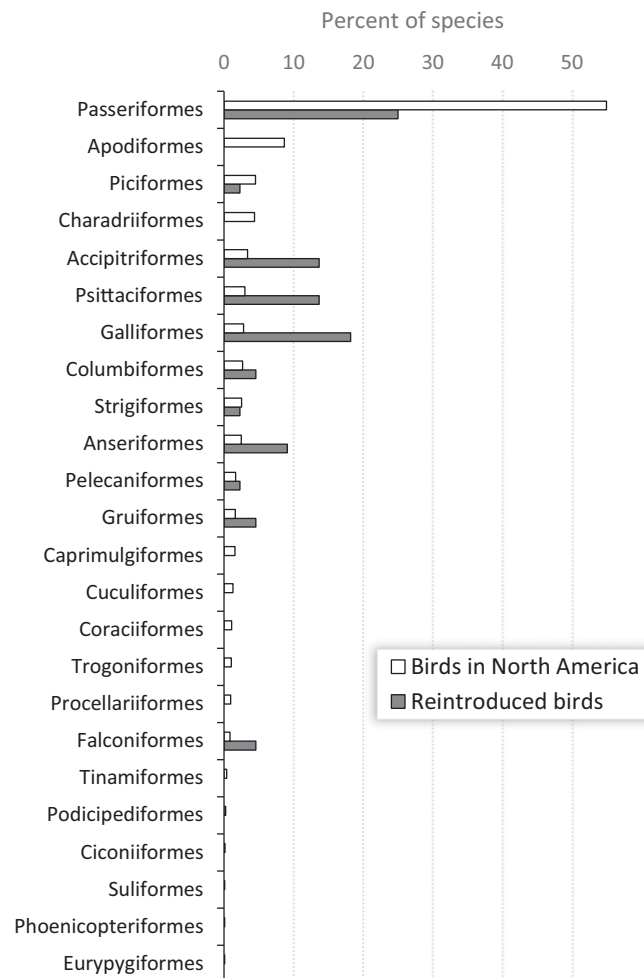**Fig. 4.** Taxonomic distribution of reintroduced species within the different orders of the terrestrial birds out of the 1,748 species of North America (including Mexico, Central America, and the Caribbean). Unshaded bars are proportions of birds out of the 1,748 species of North America, and shaded bars are the proportions of birds out of the 44 reintroduced species.

Thévenin et al.

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Table 1. PD scores of reintroduced birds and mammals and the associated expected value and SD of PD for a given subset size and a regional phylogenetic tree

Group	Subcontinent	No. of native terrestrial species	No. of reintroduced species	PD of reintroduced species	Expected PD	SD of PD	P value
Mammals	Europe	202	28	1,080.42	1,259.96	96.49	0.063
	North America	838	42	1,387.4	1,741.61	145.36	**0.015**
Birds	Europe	378	37	1,422.62	1,592.57	107.54	0.114
	North America	1,748	44	1,592.11	1,818.95	131.98	0.086

Deviation from the null model is presented as a P value, which was computed using the *pnorm* function in R. Bold values indicate $P < 0.05$.

scores are negatively related to the size of a clade, the different patterns observed between the two regions can be explained by the prevalence of members of the order Passeriformes in North American-reintroduced birds. Within mammals, while reintroduced species with the highest ED in North America come from less diverse clades (as for birds), the high median ED observed for reintroduced European mammals was largely driven by highly evolutionarily distinct species of rodents (Table S3).

Overall, our results suggest that, while reintroduced species tend to be more evolutionarily distinct, the overall contribution of the focal subset of reintroduced species to the regional phylogenetic diversity is low because the species composing these focal subsets are less phylogenetically complementary than expected under a random model (see discussions in refs. 13 and 31).

Decision Processes and Phylogenetic Patterns of Reintroductions. Our null model was built to evaluate the departure of the observed process from a basic random process. Such a random process implies that every terrestrial species in the regional assemblage has the same chance of being selected for reintroduction, which constitutes a reference model but not a realistic expectation. Indeed, although it has been suggested that reintroductions of mammals and birds target a minority of globally threatened species (8, 28), local extirpation biases may exist with respect to phylogeny (32–34). Furthermore, logical decision processes about which species to reintroduce not only necessarily consider the priority of the species for recovery (of which evolutionary history is only one component) but also consider the probability that management will be successful and the likely economic and ecological costs of the program (e.g., translocation and ongoing management costs, demographic cost to the source population) (22, 35, 36). While any locally extinct species can benefit from a reintroduction effort, these competing interests and practical limitations can impose constraints on the combinations of traits of reintroduced species. For example, body size can be hypothesized as a trait that influences the ability to garner public and political support (e.g., large-bodied species are more emblematic), the ability to successfully breed in captivity (e.g., facilitated with small-bodied species) or the ability to plan translocations (e.g., large-bodied species require large home

ranges). In that context, reintroduced species could encompass a nonrandom combination of traits, and characterizing the various constraints imposed on the implementation of reintroduction programs would allow researchers to build more relevant null models to investigate the phylogenetic structure expected for reintroduced species. This would be the first step required if we want reintroduced species to be representative of the phylogenetic diversity within an assemblage.

Geographic Scales of Decisions. Identifying gaps between the optimized allocation of conservation resources and the current allocation levels requires the consideration of the potential mismatch between global priority setting and actual implementations of conservation actions that largely depend on local practitioners and decision makers reaching consensus (37, 38). This spatial implication of conducting conservation planning at different scales has been well studied in the context of managing protected areas under the systematic conservation planning framework (10, 39, 40), but it remains relatively unexplored in the context of population restorations. Evolutionary distinctiveness measures and PD approaches in conservation prioritization differ conceptually, even if they both rely on information on evolutionary relationship between species (41). Whether PD- or ED-based approaches for conservation prioritization will ensure the best preservation of the Tree of Life under current management practice is beyond the scope of our paper. However, it is important to consider which prioritization scheme can be more easily implemented at the management level. Reintroduction practitioners designing species-specific programs are more likely to integrate "evolutionary value" through evolutionary isolation measures as these are more flexible and can be compared with other individual measures of species value (e.g., cost of recovery or probability of success) that might influence decision-making processes. However, actual reintroduction practices rely on a parochial approach to conserving species, and while opportunities to restore locally extirpated species should always merit our concern and action, incentives for restoring local diversity will not guarantee the preservation of overall regional/global diversity (13, 42). International coordination might operate at the European level (e.g., the Life Program funded by the European Commission) but is less likely to be achieved across North

Table 2. Median ED scores of each focal subset of reintroduced mammal and bird species in Europe and North America

Group	Subcontinent	No. of reintroduced species	Median ED of reintroduced species	Expected median ED	SD of median ED	P value
Mammals	Europe	28	20.84	16.6	1.74	**0.018**
	North America	42	13.46	9.25	1.05	**<0.0001**
Birds	Europe	37	19.81	15.48	1.9	**0.047**
	North America	44	8.76	8.75	1.1	0.99

Expected median ED and SD were obtained after drawing 10,000 random sets of species of the same size from the associated phylogeny. The deviation from the null model is presented as a P value, computed as 2*(Number of sampled median ED values > Median ED of reintroduced species)/(Number of samples drawn). Bold values indicate $P < 0.05$.

Thévenin et al.

America, Central America, and the Caribbean. Here, our aim was not to advocate for a systematic allocation of reintroduction efforts toward the broad-scale maximization of phylogenetic diversity. Rather, our objective was to emphasize how this phylogenetic framework can help evaluate the potential conservation benefit of reintroductions at any spatial scale. This framework simply relies on estimating the relative contribution of a single species or a subset of species (e.g., reintroduced species) to the diversity of features within any given assemblage (13); thus, the framework can be applied at local, national, regional, or global scales (43).

The development of reintroduction biology over recent decades was built on the combination of knowledge from locally implemented programs to produce insights that inform the worldwide practice of reintroduction (6, 44, 45). In addition, the recent exponential increase in the number of implemented programs provides opportunities to assess the relevance of the allocation of reintroduction efforts at different spatial scales. Reintroduction is primarily an attempt to restore locally extirpated species and, in turn, contributes to limiting the loss of feature diversity at local and global scales. Reintroduction can also be used as a powerful tool to restore the spontaneous dynamics of genes and the functional traits of the focal species that could shape community and ecosystem dynamics, thus supporting evolutionary processes. Incorporating evolutionary considerations into reintroduction planning allows us to ponder the type of diversity we are trying to restore and reminds us that conservation translocations fundamentally aim to restore evolutionary trajectories for the target species and its biotic environment (2).

Materials and Methods

Study Area and Reintroduced Species. We focused on birds and mammals because these groups benefit from the best coverage in the peer-reviewed and gray reintroduction literature, leading to the substantial availability of data (5, 46). Our study area covered the European peninsula and North and Central America (including Mexico and the Caribbean, but hereafter called North America), which are two regions where nearly 40% of worldwide translocation programs have been implemented (3). In each subcontinent, we considered the lists of terrestrial breeding bird species established by BirdLife (i.e., Europe: 378 species; North America: 1,748 species; datazone.birdlife.org/species/search), and the IUCN lists of terrestrial mammal species (i.e., Europe: 202 species; North America: 838 species; www.iucnredlist.org/). We built four regional phylogenetic trees based on these lists and from global phylogenies of all extant birds and mammals. We used updated phylogenies for mammals (47, 48), where polytomies were resolved (49), and where the Carnivora clade was replaced with a highly resolved supertree that was published more recently (24, 50). For birds, we used the global bird phylogenies built and published by Jetz et al. (51), available at www.birdtree.org.

Species were included in reintroduction efforts, and thereafter called "reintroduced species," if they had been involved in any past or ongoing documented release of individuals that satisfies the reintroduction definition provided by the IUCN *Guidelines for Reintroductions*, which was published in 2013 (4), regardless of the success of the reintroduction. Bird and mammal species that have been reintroduced at least once in Europe were identified through a comprehensive search of translocation-related publications. We conducted our research using both the ISI Web of Science database and Google Scholar, as the latter can provide references from the gray literature, which contains a substantial amount of information regarding reintroduction projects. We used the keywords "*reintroduc*,*" "*re-introduc*,*" "*translocat*,*" and the species' Latin name, and we checked independently for each European bird and mammal species (Table S1). For each query, we looked for at least one reference that would provide evidence that the species had been involved in at least one movement-and-release event that satisfied the IUCN definition of a reintroduction. Although this is not a systematic review (52, 53), we applied the same methods to locate and use information from scientific and nonscientific sources and used a rigorous, transparent, and repeatable protocol. Our results provide a detailed picture of the taxonomic distribution of reintroduction efforts of terrestrial mammals and birds in Europe that can be compared with other reviews on this topic (54). Acknowledging that we only

used English sources and that publication biases may exist (with respect to taxa, country, etc.), our literature search might have led to an underestimation of the number of reintroduced species in Europe. We extracted the list of reintroduced terrestrial breeding birds and mammals in North America from the review published by Brichieri-Colombi and Moehrenschlager (28) on animal conservation translocations. We did not consider subspecies separately in our analyses since our phylogenetic trees did not provide relationships between taxa at the subspecies level. Consequently, species were considered as reintroduced as long as one of their subspecies had been reintroduced at least once. In our final analyses, we considered 67 reintroduced terrestrial mammals (i.e., 25 in Europe, 39 in North America, 3 in both) and 79 reintroduced terrestrial breeding birds (i.e., 35 in Europe, 42 in North America, 2 in both) (Table S2).

Phylogenetic Diversity of Reintroduced Species. The phylogenetic diversity quantifies the cumulated amount of independent evolutionary histories of a subset of species in a tree (14). Given one phylogenetic tree, the PD of a subset of species is measured as the sum of the length of the branches in the minimal subtree connecting all of the taxa of the subset:

$$PD(\text{tree}) = \sum_j L_j,$$

with L_j representing the length of branch j. For a given number of species, the higher the value of PD for a subset of species, the more evolutionarily distant the species are within the subset. For each taxonomic group in each region, we calculated the total unrooted PD of the subset of reintroduced species [PD_{reint}] using the *pd.query* function from the package *PhyloMeasures* (55). We compared this value to the PD value expected for a random subset of species of the same size in the associated regional species pool (e.g., European birds, North American mammals). For that purpose, we used the *pd.moments* function, which provides optimized algorithms to compute the exact expressions of the expectation [μPD] and the SD [sdPD] of the PD for a given number of species in a specific phylogenetic tree. A subset of reintroduced species can be considered as representative of the regional phylogenetic diversity if the PD_{reint} value does not significantly depart from the associated 95% confidence interval calculated as $\mu PD \pm 1.96 * sd PD$.

Evolutionary Distinctiveness of Reintroduced Species. We measured the evolutionary isolation of individual species using the ED, which is based on the fair-proportion index that quantifies how few relatives a species has and how phylogenetically distant those relatives are (20). The ED score of species i is the total branch length between each node connecting the tip (species) to the root of the tree, each time divided by the number of species subtending that branch:

$$ED_i = \sum_{j \in P(i, \text{Root})} \frac{L_j}{n_j},$$

with $P(i, \text{Root})$ being the set of branches connecting species i to the root of the tree, and n_j being the number of species subtending branch j. We used the *evol.distinct* function from the *ape* package (56) to calculate the ED scores for mammals and birds in each regional phylogeny. We assessed whether reintroduced species were more or less evolutionarily distinct than expected if species were randomly drawn from the regional pool. We used the median ED of the subset of reintroduced species rather than the mean given the skewness of the distribution of ED scores, and compared the median ED to the 95% confidence interval of the null distribution obtained by drawing 10,000 random samples of species of the same size in the associated regional phylogeny. The departure from the expected median ED produced by our null model was expressed as a *P* value and was calculated as the number of random median ED values that were superior to the median ED of reintroduced species and divided by the number of randomly drawn subsets.

We tested the deviation from our null model for both metrics of each set of reintroduced species (i.e., terrestrial mammals or terrestrial breeding birds) on each subcontinent (i.e., Europe or North America). In each case, the analyses were run using 100 fully resolved regional phylogenetic trees. All results provided are the median of the values taken across the 100 phylogenetic trees. All analyses were compiled with R 3.2.2.

Thévenin et al.

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1. Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc Natl Acad Sci USA* 114:E6089–E6096.
2. Sarrazin F, Lecomte J (2016) Evolution in the Anthropocene. *Science* 351:922–923.
3. Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP (2014) Reversing defaunation: restoring species in a changing world. *Science* 345:406–412.
4. IUCN/SSC (2013) *Guidelines for Reintroductions and Other Conservation Translocations* (IUCN Species Survival Commission, Gland, Switzerland).
5. Fischer J, Lindenmayer DB (2000) An assessment of the published results of animal relocations. *Biol Conserv* 96:1–11.
6. Seddon PJ, Armstrong DP, Maloney RF (2007) Developing the science of reintroduction biology. *Conserv Biol* 21:303–312.
7. Graham MF, Veitch CR (2002) Changes in bird numbers on Tiritiri Matangi Island, New Zealand, over the period of rat eradication. *Turning the Tide: The Eradication of Invasive Species* (International Union for Conservation of Nature and Natural Resources, Auckland, New Zealand), pp 120–123.
8. Seddon PJ, Soorae PS, Launay F (2005) Taxonomic bias in reintroduction projects. *Anim Conserv* 8:51–58.
9. Mace GM, Gittleman JL, Purvis A (2003) Preserving the tree of life. *Science* 300:1707–1709.
10. Margules CR, Pressey RL (2000) Systematic conservation planning. *Nature* 405:243–253.
11. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858.
12. Vane-Wright RI, Humphries CJ, Williams PH (1991) What to protect?—Systematics and the agony of choice. *Biol Conserv* 55:235–254.
13. Faith DP (2016) A general model for biodiversity and its value. *The Routledge Handbook of Philosophy of Biodiversity* (Routledge, New York).
14. Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biol Conserv* 61:1–10.
15. Forest F, et al. (2007) Preserving the evolutionary potential of floras in biodiversity hotspots. *Nature* 445:757–760.
16. Winter M, Devictor V, Schweiger O (2013) Phylogenetic diversity and nature conservation: where are we? *Trends Ecol Evol* 28:199–204.
17. Rosauer DF, Mooers AO (2013) Nurturing the use of evolutionary diversity in nature conservation. *Trends Ecol Evol* 28:322–323.
18. Veron S, Davies TJ, Cadotte MW, Clergeau P, Pavoine S (2017) Predicting loss of evolutionary history: Where are we? *Biol Rev Camb Philos Soc* 92:271–291.
19. Cadotte MW, Jonathan Davies T (2010) Rarest of the rare: Advances in combining evolutionary distinctiveness and scarcity to inform conservation at biogeographical scales. *Divers Distrib* 16:376–385.
20. Isaac NJ, Turvey ST, Collen B, Waterman C, Baillie JE (2007) Mammals on the EDGE: conservation priorities based on threat and phylogeny. *PLoS One* 2:e296.
21. Volkmann L, Martyn I, Moulton V, Spillner A, Mooers AO (2014) Prioritizing populations for conservation using phylogenetic networks. *PLoS One* 9:e88945.
22. Nunes LA, Turvey ST, Rosindell J (2015) The price of conserving avian phylogenetic diversity: A global prioritization approach. *Philos Trans R Soc Lond B Biol Sci* 370:20140004.
23. Hipp AL, et al. (2015) Phylogeny in the service of ecological restoration. *Am J Bot* 102:647–648.
24. Thuiller W, et al. (2015) Conserving the functional and phylogenetic trees of life of European tetrapods. *Philos Trans R Soc Lond B Biol Sci* 370:20140005.
25. Sobral FL, et al. (2014) Spatial conservation priorities for top predators reveal mismatches among taxonomic, phylogenetic and functional diversity. *Nat Conserv* 12:150–155.
26. Guilhaumon F, et al. (2015) Representing taxonomic, phylogenetic and functional diversity: New challenges for Mediterranean marine-protected areas. *Divers Distrib* 21:175–187.
27. Tucker CM, et al. (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol Rev Camb Philos Soc* 92:698–715.
28. Brichieri-Colombi TA, Moehrenschlager A (2016) Alignment of threat, effort, and perceived success in North American conservation translocations. *Conserv Biol* 30:1159–1172.
29. Fritz SA, Purvis A (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conserv Biol* 24:1042–1051.
30. Converse SJ, Armstrong DP (2016) Demographic modeling for reintroduction decision-making. *Reintroduction of Fish and Wildlife Populations* (University of California Press, Oakland, CA), pp 123–146.
31. Faith DP, Carter G, Cassis G, Ferrier S, Wilkie L (2003) Complementarity, biodiversity viability analysis, and policy-based algorithms for conservation. *Environ Sci Policy* 6:311–328.
32. May-Collado LJ, Agnarsson I (2011) Phylogenetic analysis of conservation priorities for aquatic mammals and their terrestrial relatives, with a comparison of methods. *PLoS One* 6:e22562.
33. Arregoitia LDV, Blomberg SP, Fisher DO (2013) Phylogenetic correlates of extinction risk in mammals: Species in older lineages are not at greater risk. *Proc Biol Sci* 280:20131092.
34. Jetz W, et al. (2014) Global distribution and conservation of evolutionary distinctness in birds. *Curr Biol* 24:919–930.
35. Joseph LN, Maloney RF, Possingham HP (2009) Optimal allocation of resources among threatened species: a project prioritization protocol. *Conserv Biol* 23:328–338.
36. Chauvenet ALM, Canessa S, Ewen JG (2016) Setting objectives and defining the success of reintroductions. *Reintroduction of Fish and Wildlife Populations* (University of California Press, Oakland, CA), pp 105–121.
37. Mace GM (2000) It's time to work together and stop duplicating conservation efforts. *Nature* 405:393.
38. da Fonseca GAB (2000) Following Africa's lead in setting priorities. *Nature* 405:393–394.
39. Rodrigues ASL, Gaston KJ (2002) Rarity and conservation planning across geopolitical units. *Conserv Biol* 16:674–682.
40. Kukkala AS, Moilanen A (2013) Core concepts of spatial prioritisation in systematic conservation planning. *Biol Rev Camb Philos Soc* 88:443–464.
41. Redding DW, et al. (2008) Evolutionarily distinctive species often capture more phylogenetic diversity than expected. *J Theor Biol* 251:606–615.
42. Hunter ML, Hutchinson A (1994) The virtues and shortcomings of parochialism: Conserving species that are locally rare, but globally common. *Conserv Biol* 8:1163–1165.
43. Redding DW, Mooers AO, Şekercioğlu ÇH, Collen B (2015) Global evolutionary isolation measures can capture key local conservation species in Nearctic and Neotropical bird communities. *Philos Trans R Soc Lond B Biol Sci* 370:20140013.
44. Sarrazin F, Barbault R (1996) Reintroduction: challenges and lessons for basic ecology. *Trends Ecol Evol* 11:474–478.
45. Armstrong DP, Seddon PJ (2008) Directions in reintroduction biology. *Trends Ecol Evol* 23:20–25.
46. Bajomi B, Pullin AS, Stewart GB, Takács-Sánta A (2010) Bias and dispersal in the animal reintroduction literature. *Oryx* 44:358–365.
47. Bininda-Emonds ORP, et al. (2007) The delayed rise of present-day mammals. *Nature* 446:507–512.
48. Fritz SA, Purvis A (2010) Phylogenetic diversity does not capture body size variation at risk in the world's mammals. *Proc Biol Sci* 277:2435–2441.
49. Kuhn TS, Mooers AØ, Thomas GH (2011) A simple polytomy resolver for dated phylogenies. *Methods Ecol Evol* 2:427–436.
50. Nyakatura K, Bininda-Emonds OR (2012) Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *BMC Biol* 10:12.
51. Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. *Nature* 491:444–448.
52. Pullin AS, Stewart GB (2006) Guidelines for systematic review in conservation and environmental management. *Conserv Biol* 20:1647–1656.
53. Davies ZG, Pullin AS (2007) Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landsc Ecol* 22:333–351.
54. Swan KD, McPherson JM, Seddon PJ, Moehrenschlager A (2016) Managing marine biodiversity: The rising diversity and prevalence of marine conservation translocations. *Conserv Lett* 9:239–251.
55. Tsirogiannis C, Sandel B (2016) PhyloMeasures: A package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography* 39:709–714.
56. Paradis E, Claude J, Strimmer K (2004) APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290.

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Thévenin et al.

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