Intentional and unintentional changes to avian and mammalian diversities in the UK

Wenyuan Zhang[1*†], Kevin J Gaston[2], Ben C Sheldon[1], and Richard Grenyer[3]

Rewilding is emerging as a promising restoration strategy to tackle the challenges posed by global change and maintain natural ecosystems and their biodiversity. However, rewilding has also been criticized for the absence of a consistent definition and insufficient knowledge about its possible outcomes. Here, we explored the effects of rewilding on filling functional gaps created by the extirpation of native species. We contrasted rewilding with three other mechanisms for change in community composition—species extirpation, species introduction, and unassisted colonization—in terms of their impacts on changes in avian and mammalian diversity in the UK. We found that (i) while rewilding increases functional diversity most on average, introduced/naturalized birds contribute more functional uniqueness to native functional space than other groups of birds; and (ii) changes in functional diversity associated with "rewilded" organisms were species-dependent and idiosyncratic. Our results suggest that although rewilding can expand or infill native functional trait space to some extent, such effects require careful assessment.

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Biodiversity has undergone fundamental alteration worldwide (Lewis and Maslin 2015), with widespread impacts on the functioning of ecosystems and uncertain outcomes. Conservation efforts, especially the establishment of protected areas, have demonstrated favorable ecological performance in slowing or halting biodiversity loss in some instances (Gaston *et al*. 2008); however, reports of possibly ineffective protected areas and ongoing declines of species suggest that long-term maintenance of biodiversity requires additional strategies (Parks *et al*. 2023). Rewilding, a special case of species (re) introduction, has been proposed as an approach to promote self-regulating ecosystems while minimizing or gradually reducing human forcing on them (Perino *et al*. 2019).

Rewilding initiatives explicitly acknowledge the role of reducing human interventions and emphasize the impacts on people's emotional experience and perception of wild nature and wild ecosystems, serving as a response to public demand for a sense of "wildness" (Perino *et al*. 2019). Therefore, rewilding can be viewed as a possible pathway that societies can take toward attaining sustainability that may generate co-benefits extending beyond natural heritage conservation (Perino *et al*. 2019). The concept of rewilding is gaining momentum and becoming increasingly influential in restoration ecology and conservation science (Perino *et al*. 2019).

Despite the potential for rewilding to address pressing restoration challenges, critics have pointed out that the uncertainty of its outcome hinders the application of rewilding principles (Nogués-Bravo *et al*. 2016). One particular obstacle is a lack of understanding of the influence of rewilding projects on filling functional gaps in extant native species pools (Nogués-Bravo *et al*. 2016). Although rewilding initiatives have been proposed and implemented on the grounds, at least in part, that reintroductions of extirpated species will have positive outcomes concerning the filling of such gaps, whether they actually do remains largely untested. With the number of rewilding initiatives growing (Perino *et al*. 2019), it is imperative that relevant assessments are developed and conducted.

Meanwhile, three other processes—species extirpation, intentional/accidental human introduction of species, and unassisted (re)colonization—can cause variation in the species composition of natural assemblages. Extirpation of species can result in functional diversity loss to different degrees across the world depending on the region and taxonomic group of interest (Toussaint *et al*. 2021). Non-native species pose a major threat to native diversity and can cause extirpations directly (eg predation and competitive displacement) or indirectly (eg pathogen introduction and cascading effects in networks), which can lead to global diversity loss (Catford *et al*. 2018). However, non-native species can also be tolerated and contribute new functions to invaded systems (Schlaepfer 2018). If phylogenetically and functionally distinct from native species, new natural colonists can add marked functional uniqueness and evolutionary history to native assemblages (Park *et al*. 2020); however, if closely related to native species, they can also add little in this regard (Daehler 2001). Despite major efforts to determine the effects of these three processes on native diversity, the extent to which rewilding can outweigh them in terms of filling native functional gaps remains unclear.

We contrasted the impacts of rewilding with species extirpation, introduction, and natural colonization on extant diversity (functional and phylogenetic) for birds and mammals in

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[1] *Edward Grey Institute, Department of Biology, University of Oxford, Oxford, UK** *(wzhang.ecoevo@gmail.com);* † *current address: Department of Biology, Quebec Centre for Biodiversity Science, McGill University, Montreal, Canada;* [2] *Environment and Sustainability Institute, University of Exeter, Penryn, UK;* [3] *School of Geography and the Environment, University of Oxford, Oxford, UK*

the UK. Successful establishment of a non-native species may alter its impacts on native species (Blackburn *et al.* 2011), and therefore we investigated the effects of species introduction by defining two groups of non-native species based on whether they have established populations in the wild. In summary, we estimated the different effects across rewilding and four other groups of novel species: (i) *rewilding species*—those that are being reintroduced and reinforced by human-mediated conservation translocation; (ii) *introduced species*—species that were introduced by humans and have bred in the wild but without establishing self-sustaining populations; (iii) *naturalized species*—species that were introduced by humans and that established self-sustaining populations; (iv) *recent (re)colonists*—those that have colonized (or re-colonized) naturally without direct human interference; and (v) *extirpated species*—those that are extinct in the UK but exist elsewhere.

We tested the influence of the five groups of novel species on extant native diversity through two processes. First, we quantified the degree to which functional and phylogenetic diversity increased when different novel species were added to the native species pool at the individual and group-average levels. Second, we measured how different groups of novel species overlap with native species in functional trait space using a hypervolume method, from which we estimated the degree of functional uniqueness that the novel species could contribute to native species assemblages.

Methods

Bird and mammal data

We composed a list of birds using data from the Avian Population Estimates Panel (APEP4) (Woodward *et al.* 2020) for the diversity evaluation. Given that wintering species exhibit less site fidelity than breeding species and the effects of non-breeding populations on local diversity are comparatively unstable (Matthiopoulos *et al.* 2005), we excluded solely wintering species from subsequent analyses. We also employed the British List (BOU 2018) to categorize species as introduced, naturalized, recently colonized, extirpated, and rewilding. Specifically, species that have bred in the wild in the UK but are not judged by the British List to have self-sustaining populations were added as introduced species. Naturalized species were defined as those included in APEP4 and listed as naturalized species on the British List, whereas recent (re)colonists were defined as species that have colonized since 1945. We classified species currently being reintroduced and reinforced by human-mediated conservation translocation as rewilding species, for which we collated data from multiple sources (see "The avian category in the UK" table in Zhang *et al.* [2024]).

For analysis of mammalian fauna, we relied on the UK Mammal List from the Mammal Society (Crawley 2020), using the classification of extant native species therein. Given that introduced and naturalized species were classified within the same category in the UK Mammal List, naturalized species were extracted from the List following Macdonald and Burnham (2010), where naturalized species were defined as those with established self-sustaining populations in the wild. Rewilding species were derived from related project websites (see "The mammal category in the UK" table in Zhang *et al.* [2024]). Because no records of recent (re)colonization by mammals in the UK were available, we excluded that category from the mammal analysis. We also excluded pinnipeds and cetaceans.

For both birds and mammals, we identified extirpated species, based on Yalden and Barrett (1999) and Yalden and Albarella (2008), since the end of the Late Glacial Maximum (around 12,000 years ago). This is approximately the time when ice sheets had retreated and sea levels had risen enough to allow re-opening of the North Sea and English Channel, separating the British Isles from mainland Europe.

Diversity

To quantify diversity change, we calculated phylogenetic and functional diversity based on presence–absence approaches. Phylogenetic distance was calculated using 100 dendrograms sampled randomly from a full pseudo-posterior distribution of phylogenetic trees (https://birdtree.org). Mean phylogenetic diversity across these 100 dendrograms was calculated, and phylogenetic diversity was taken as the sum of the total branch length of a phylogenetic tree via the root (Faith 1992). We used five traits to calculate functional diversity: body mass (quantitative), litter/clutch size (quantitative), generation length (quantitative), foraging strata of birds (proportional)/habitat breadth of mammals (quantitative), and diet (proportional). These particular traits were chosen because they were believed to characterize a large portion of the Eltonian niches of species (Wilman *et al.* 2014). For birds, we opted for foraging stratum instead of habitat breadth because the former can provide additional information about foraging behavior and aids in prediction of relatively detailed ecological processes (Beauchamp and Mangini 2024). We then calculated functional distance using a multivariate trait dissimilarity of Gower's distance (Gower 1971; Pavoine *et al.* 2009) for each pairwise species. This was followed by the construction of neighbor-joining trees (Cardoso *et al.* 2024), which build functional dendrograms in a way similar to the construction of phylogenetic trees and thus provide a means of comparing functional and phylogenetic diversity (Cardoso *et al.* 2024). Finally, functional diversity was calculated as the summed branch lengths of the functional dendrogram (Petchey and Gaston 2002).

We assessed the influence of novel species on native diversity at both the individual and group-average levels. For individual effect, we calculated native functional and phylogenetic diversity, followed by the diversity change after adding each individual novel species. For individual novel species i, we calculated the relative diversity change d_i by dividing the diversity change using the null diversity change, and we scaled relative diversity changes d_i from 0 to 1 using $d_i = \frac{d_i - \min(d)}{\max(d) - \min(d)}$, where d_i is the standardized diversity change for species i, $\min(d)$ is the minimum of all relative diversity changes, and $\max(d)$ is the maximum of all relative diversity changes.

By calculating the standard effect size, we also estimated whether diversity change for each novel species group was larger on average than expected. To do so, we added each group of novel species to the native species pool, calculated the diversity change, and compared this result with those derived from null models. To construct the null models, for each group of novel species, we randomly selected species from the novel species pool until the total of selected species matched the number of species present in the focal group, added the randomly selected species to the native species pool, and then calculated the diversity change. This process was repeated 1000 times. We used a non-parametric measure of standard effect size between observed diversity change and diversity change derived from the null models to indicate the average performance of target novel species in increasing diversity relative to expectations.

Hypervolume estimation

We used hypervolume analysis (Blonder 2018) to estimate how different groups of introduced, naturalized, recent (re)colonized, rewilding, and extirpated species overlap with native species in the functional trait space (that is, how much functional uniqueness the novel species contribute to native species). A hypervolume was constructed for each group of novel and native species using the one-class support vector machine (SVM) estimation method (Blonder 2018; Cooke *et al.* 2019). SVM provides a smooth fit around the data that is robust to outliers, yields a binary boundary classification ("in" or "out"), is invariant to rotational transformation (ie correlations between axes), and is computationally viable for large datasets and high dimensional hyperspaces (Blonder 2018). Because analyses with few observations are likely to be biased and not recommended for hypervolume analysis (Blonder 2018), results were excluded when the number of species within a given group was lower than the number of traits.

We assessed pairwise overlap among the hypervolumes by calculating the unique and overlapped volume fraction of each pair of hypervolumes (Blonder 2018). Specifically, we assessed pairwise overlap between native species and each group of introduced, naturalized, recent (re)colonized, rewilding, and extirpated species (five paired hypervolumes in total), and so we used the fraction of functional space that was not occupied by native species to evaluate the functional uniqueness that groups of novel species contributed to native assemblages of species. Although comparative statistics are influenced by sample size (Blonder 2018), we were interested in the total volume of trait space occupied by each introduced, naturalized, recent (re)colonized, rewilding, and extirpated species relative to the entire trait space occupied by native species, and thus we relied on the original sample size in this analysis.

For the hypervolume overlap analysis, we calculated continuous measures for a species' diet and foraging strata based on semi-quantitative records of seven diet and seven foraging strata categories. This resulted in two combining traits (diet and foraging) and three original traits (body mass, litter/clutch size, and generation length). Specifically, we first calculated the Gower distance (Gower 1971) between species based on the diet or foraging strata data following a principal component analysis. We used the first principal component as synthetic trait values in the trait space and hypervolume analyses, which captured 38.6% of diet and 41.1% of foraging strata variation for birds and 53.4% of diet and 24.5% of foraging strata variation for mammals. These proportions represent the relative importance of diet or foraging strata in the initial dataset (Cooke *et al.* 2019). Conversion to unitless coordinates was required so that volumes or overlaps could be defined. We therefore first transformed trait data to improve normality: $\log_{10}$ for body mass, generation length, and litter/clutch size, and square root for habitat breadth; we then standardized all traits using a z transformation. Therefore, values of each trait had a mean and a standard deviation (SD) of 0 ± 1, and the volume of trait space is given in SD units of transformed trait values raised to the power of the number of traits considered (in this case, five: therefore SD^5) (Cooke *et al.* 2019).

Results

While the influence of novel species on extant native diversity varied considerably within and across each group, general patterns emerged. Adding both rewilding and introduced species to the native bird assemblages increased functional diversity more than expected (standard effect size: 1.15 for rewilding birds and 0.39 for introduced birds; Table 1). Rewilding, recent (re)colonists, and extirpated birds increased phylogenetic diversity more than expected, whereas introduced and naturalized species increased phylogenetic diversity less than expected (Figure 1b). Adding naturalized species increased the functional diversity of native bird assemblages to a greater degree than by adding recent (re)colonists and extirpated species (Figure 1a). When added to native bird assemblages, recent avian (re)colonists contributed the least amount of change in functional diversity (standard effect size: –2.39; Table 1; Figure 1a).

For mammals, reintroducing extirpated species and rewilding species had the largest effect on functional diversity as compared to reintroducing other groups of novel mammal species (standard effect size: 0.11 for extirpated and 0.32 for rewilding mammals in average functional diversity change; Table 1; Figure 2a), while naturalized species had the smallest effect on average functional diversity (standard effect size: –0.91). Although only two mammal species were classified as introduced, they had largest effect on phylogenetic diversity

Table 1. Effects of introduced, naturalized, rewilding, recent (re)colonist, and extirpated species on extant native diversity measured by functional diversity, phylogenetic diversity, and hypervolume space

Taxa	Measures	Introduced	Naturalized	Rewilding	Recent (re) colonist	Extirpated
Birds	Number of species	26	18	14	11	6
	Avg functional diversity change (SES)	0.39	–0.15	1.15	–2.39	–0.43
	Avg phylogenetic diversity change (SES)	–1.83	–2.48	3.29	–0.22	0.14
	Unique functional space (SD^5)	3.6	0.5	1.1	0.4	0.02
Mammals	Number of species	2	12	7	0	12
	Avg functional diversity change (SES)	–0.80	–0.91	0.32	–	0.11
	Avg phylogenetic diversity change (SES)	2.02	–1.50	0.79	–	–1.33
	Unique functional space (SD^5)	–	6.4	0.3	–	1.5

Notes: Avg: average; SES: standard effect size; SD^5: units of the unique and overlapping fractions.

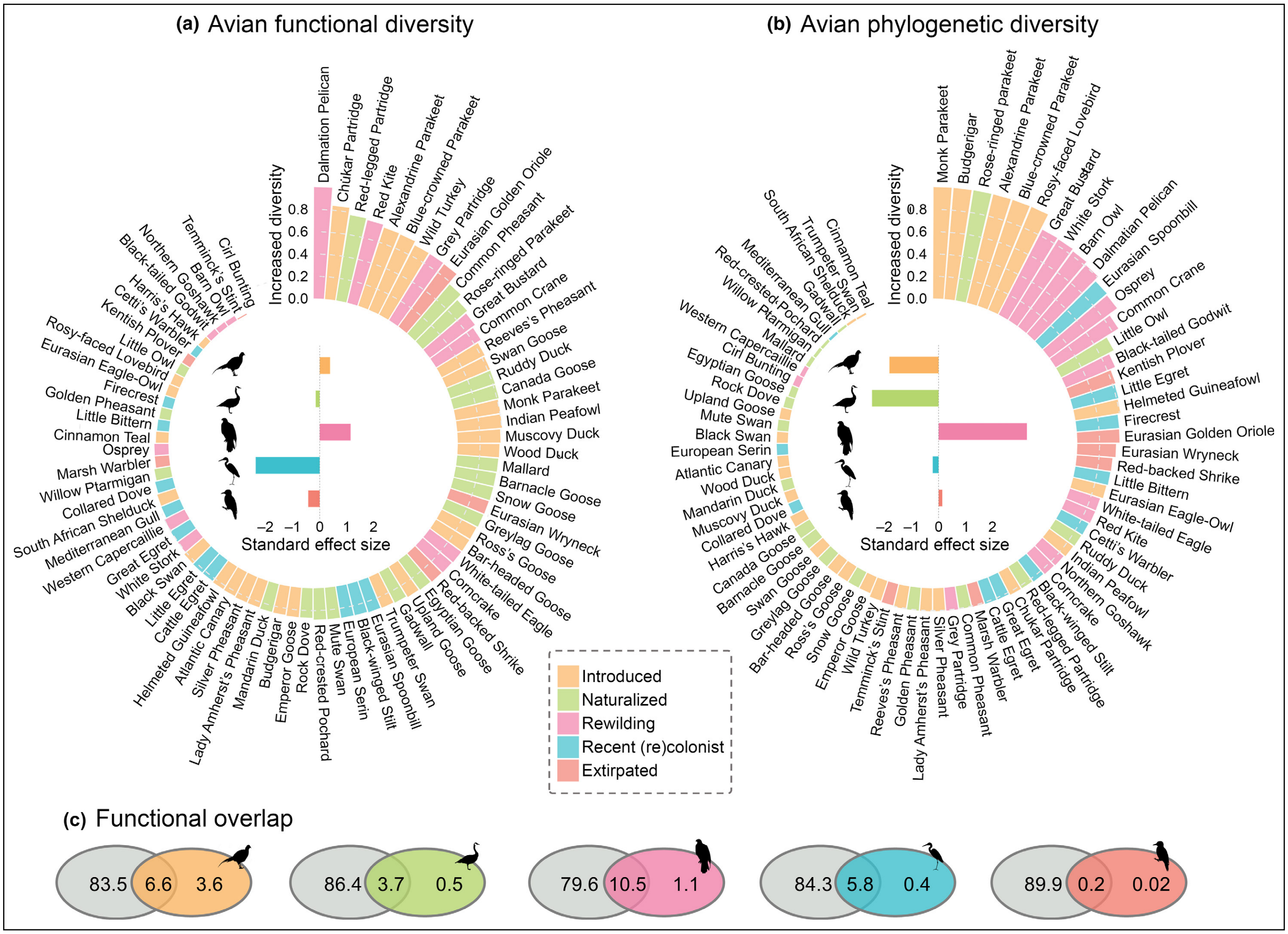

Figure 1. Influence of introduced, naturalized, rewilding, recently (re)colonized, and extirpated species on native bird diversity. Bar height indicates the increase in native (a) functional diversity and (b) phylogenetic diversity when adding an individual introduced, naturalized, rewilding, recently (re)colonized, or extirpated species to native assemblages of species, standardized to vary from 0 to 1. Colors represent different species groups (see key). (c) Two-dimensional representation of the overlap in five-dimensional trait space. Different colors represent different species groups: native (gray, full volume ~92 SD^5), introduced (yellow, full volume ~10 SD^5), naturalized (turquoise, full volume ~5 SD^5), rewilding (purple, full volume ~6 SD^5), recent (re)colonists (blue, full volume ~6 SD^5), and extirpated (red, full volume ~0.4 SD^5). Hypervolumes for each group of species were constructed from five *z*-transformed traits: $\log_{10}$ (body mass), $\log_{10}$ (clutch size), $\log_{10}$ (generation length), diet, and foraging strata. Units for the unique and overlapping fractions are expressed as SD^5 (see main text). Bird silhouettes (www.phylopic.org, CC0 1.0 Public Domain) depict examples of different species groups.

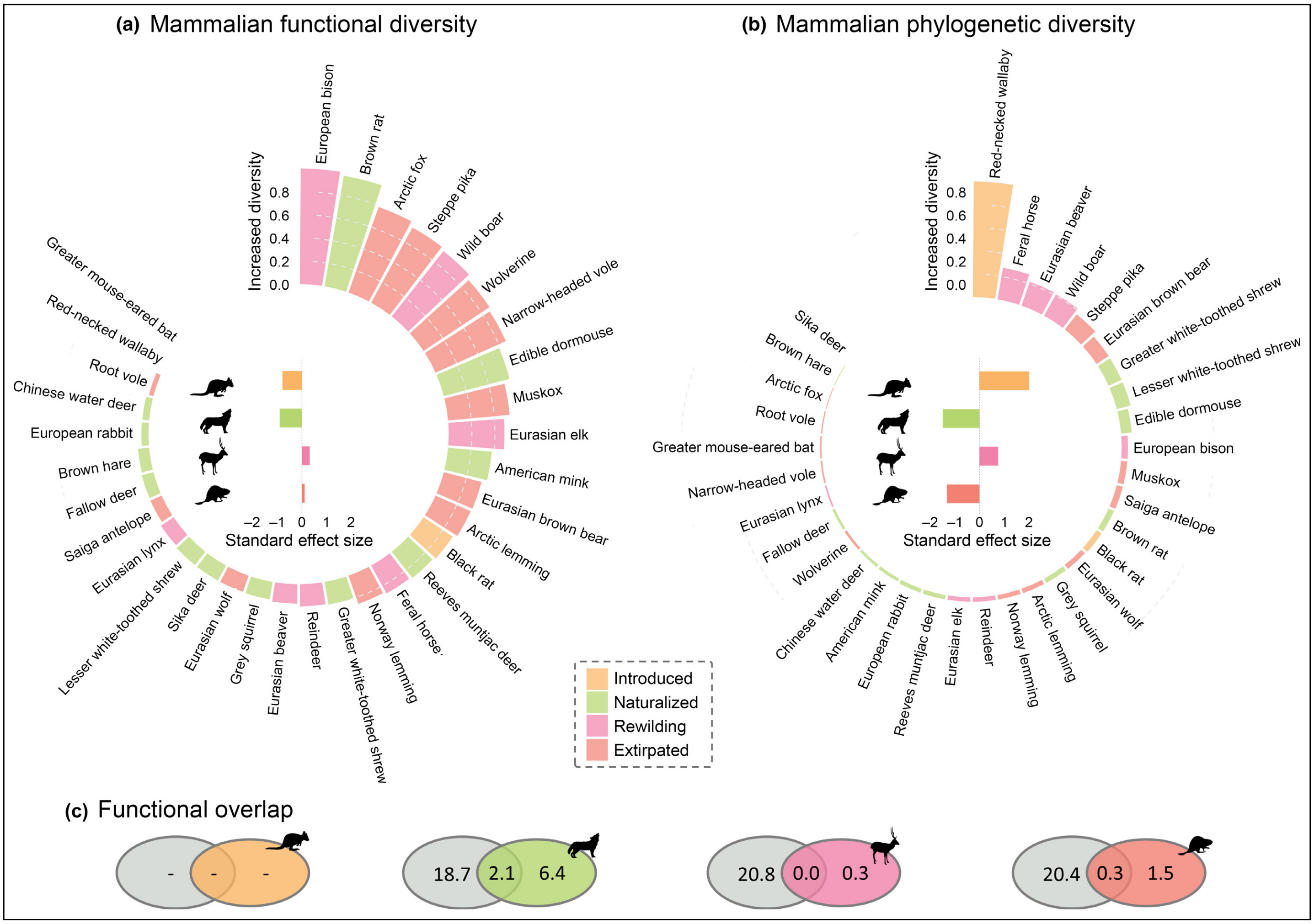

Figure 2. Influence of introduced, naturalized, rewilding, and extirpated species on native mammal diversity. Bar height indicates the increase in native (a) functional diversity and (b) phylogenetic diversity when adding an individual introduced, naturalized, rewilding, or extirpated species to native assemblages of species, standardized to vary from 0 to 1. Colors represent different species groups (see key). (c) Two-dimensional representation of the overlap in five-dimensional trait space. Different colors represent different species groups: native (gray, full volume ~20 SD^5), introduced (yellow, full volume not available as the number of species is less than the number of traits), naturalized (turquoise, full volume ~9 SD^5), rewilding (purple, full volume ~ 0.3 SD^5), and extirpated (red, full volume ~3 SD^5). Hypervolumes for each group of species were constructed from five *z*-transformed traits: $\log_{10}$ (body mass), $\log_{10}$ (litter size), $\log_{10}$ (generation length), square root (habitat breadth), and diet. Units for the unique and overlapping fractions are expressed as SD^5 (see main text). Mammal silhouettes (www.phylopic.org, CC0 1.0 Public Domain) depict examples of different species groups.

(standard effect size: 2.02; Figure 2b). On average, adding naturalized species to the native mammal assemblage resulted in the least amount of change in phylogenetic diversity (standard effect size: –1.50; Table 1).

Introduced bird species had the largest functional trait space that was unoccupied by native bird species (unique volume = 3.6 SD^5; Figure 1c), followed by rewilding bird species (1.2% of the combined volume 91.1 SD^5). Extirpated species had the least unique space as compared with native species (0.02% of the combined volume 90.1 SD^5). Naturalized species occupied 0.5% of combined space unoccupied by native species (unique volume = 0.5 SD^5), followed by recent (re)colonists (unique volume = 0.4 SD^5). Recent (re)colonists had the largest proportion of overlap with native bird species in terms of functional trait space. The overlapping space accounts for 94.2% (intersection volume = 5.8 SD^5) of the functional trait space of recent (re)colonists (full volume = 6.2 SD^5).

As compared with birds, mammals exhibited different patterns of relative occupation of functional trait space by groups (Table 1; Figure 2c). Naturalized mammal species had the largest space that was unoccupied by native species (unique volume = 6.4 SD^5). Rewilding mammals had the least space unoccupied by (unique volume = 0.3 SD^5) and the least overlap with (intersection volume = 0.0 SD^5) native species. Extirpated mammal species occupied 6.8% of space (unique volume = 1.5 SD^5) unoccupied by native species (combined volume 22.3 SD^5).

Discussion

Here, we demonstrate the relative impact on functional and phylogenetic diversities of adding different individual species and groups of novel avian and mammalian species (ie rewilding, introduced, naturalized, recent [re]colonized, and extirpated species) to native assemblages of species. Despite a potential for species that currently comprise rewilding options in the UK to increase functional diversity on average to a greater degree than those brought in by other processes, in total rewilding species contribute less functional uniqueness as compared with introduced species. Moreover, the overall effects of rewilding on filling functional gaps were species-specific and idiosyncratic.

We found that rewilding species (both birds and mammals) contribute less to functional uniqueness than naturalized and introduced species, an indication that human introductions of species tend to include species with more dissimilar functional traits than native species, perhaps because their "exotic" nature is a common driver for the processes that lead to introductions. Conservation targets aiming at filling functional gaps thus might not be most effectively addressed by rewilding programs as currently envisaged. At the same time, however, rewilding birds contributed more functional uniqueness to extant native species than recent (re)colonists. These results suggest that an intervention approach is still important if filling functional gaps is a goal. This can be viewed from two perspectives. First, recent (re)colonists shared more functional traits with extant native species, and therefore their trait combinations did not fill much additional niche space. This suggests that recent (re)colonists tend to follow a preadaptation naturalization hypothesis (ie non-native species closely related to native species would be more likely to colonize naturally, given the potentially similar adaptations to local environments they share with native species; Daehler 2001). Second, rewilding, as a human-mediated approach, was more effective at filling functional gaps than natural colonization, indicating that some distinct niches in functional space were filled by rewilding species—which, in total, are morphologically diverse—and cannot be filled by the process of natural colonization. Likewise, rewilding birds contributed more functional uniqueness than extirpated birds, which also suggests that rewilding programs were trying to reintroduce species that were more functionally distinct; consequently, extirpated species (which have fewer distinct functional traits relative to their rewilding counterparts) have not been reintroduced in rewilding programs.

Recent and potential community changes were found to differ between birds and mammals, most notably in the effects of reintroducing extirpated species. On average, reintroducing extirpated bird species increased the functional diversity of native assemblages by an amount that ranked next to last overall, while reintroducing extirpated mammal species contributed more functional uniqueness than rewilding mammal species. These outcomes could potentially be explained as consequences of the large variance in individual-level functional traits in rewilding species (ie relative to other species, although some rewilding species increase functional diversity by a greater degree, half of rewilding species increase functional diversity by a lesser degree). This also highlights the necessity of assessing the species-dependent effects of rewilding projects if filling functional gaps is the main objective.

Moreover, species-dependent effects on phylogenetic diversity tended to be stronger than those on functional diversity. For example, the red-necked wallaby (*Macropus rufogriseus*), an introduced species, increased total phylogenetic diversity the most. This suggests that even a limited number of species with distinct evolutionary histories can strongly influence phylogenetic diversity.

We focused on the impacts of rewilding on the functional and phylogenetic diversity of birds and mammals in the UK, with the recognition that such impacts might differ for other taxa in other regions. However, the UK is characterized by having comparatively well-known assemblages of species, as well as non-trivial numbers of naturalized species and multiple rewilding projects in progress or under consideration. Consequently, our findings here may have implications for other regions in terms of the importance of considering species-dependent effects if rewilding programs are proposed. We show that the contribution of rewilding species could be highly dependent on how species with more complicated local histories (archaeo-introductions, population reinforcement, and uncertain reproductive status) are viewed. Our results provide important insights for conservation translocation rewilding programs, and underscore that rewilding programs require careful assessment if filling of functional gaps is a primary goal.

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Data Availability Statement

Data and code (Zhang *et al.* 2024) are available on Figshare at https://doi.org/10.6084/m9.figshare.25208960.

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