RESEARCH ARTICLE

Shifts in ecosystem equilibria following trophic rewilding

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Abstract

Aim: Trophic rewilding is proposed as an approach to tackle biodiversity loss by restoring ecosystem dynamics through the reintroduction of keystone species. Currently, evidence on the ecological consequences of reintroduction programmes is sparse and difficult to generalize. To better understand the ecological consequences of trophic rewilding, we simulated the extinction and reintroduction of large-bodied mammals under different environmental conditions.

Location: Europe.

Methods: We selected four locations varying in productivity and seasonality in Europe and used a general ecosystem model called Madingley to run simulations. We initialized the model using body mass limits of a European Holocene baseline; we then removed large mammals and let the model converge to a new equilibrium. Next, we reintroduced the previously removed groups to assess whether the equilibrium would shift back to the initial condition. We tested three different reintroduction scenarios, in order to disentangle the importance of the different large mammal groups.

Results: The removal of large-bodied mammals led to cascading effects, mainly resulting in increases in smaller-bodied herbivores and the release of mesopredators. Post-reintroduction, the system's new equilibrium state was closer to the initial equilibrium for stable and productive locations compared to highly seasonal and low-productive locations. The maximum trait space volume of the initial state and the post-reintroduction state varied by 9.1% on average over all locations, with an average decrease in trait combinations of 6.6%. The body mass distribution differed by 28%, comparing the initial state to the post-reintroduction state.

Main Conclusions: Our simulation results suggest that reintroducing locally extinct large-bodied mammals can broadly restore shifts in ecosystem structure, roughly resembling the baseline ecosystem conditions. However, the extent to which the ecosystem's state resembles the original ecosystem is largely dependent on the reintroduction strategy (only herbivores and omnivores vs. also carnivores) and timing, as well as local environmental conditions.

1 | INTRODUCTION

The last ~100,000 years (the late Quaternary) have been characterized by numerous extinctions and substantial changes in communities' structure and composition, affecting ecosystem integrity and functioning across the globe (Blowes et al., 2019; Smith et al., 2018; Turvey & Crees, 2019). Many studies suggest that the loss of large-bodied mammals has triggered changes in species diversity, vegetation and ecosystem structure, as well as biogeochemical cycling of ecosystems (Doughty et al., 2010; Doughty, Faurby, & Svenning, 2016; Doughty, Roman, et al., 2016; Enquist et al., 2020; Faurby & Svenning, 2015; Malhi et al., 2016). As part of rewilding strategies to mitigate the loss of biodiversity and restore self-regulating ecosystems, trophic rewilding aims to restore self-regulating ecosystems by reintroducing locally extinct (or functionally analogous) keystone species (Svenning et al., 2016), which are expected to recover ecosystem dynamics that have gone lost following their extinction (Corlett, 2016a; Lundgren et al., 2018; Seddon et al., 2014; Smith et al., 2016; Soulé & Noss, 1998). Initially, rewilding was focused on bringing back large carnivores to restore the natural top–down control mechanisms and the associated trophic cascades (Soulé & Noss, 1998). In later projects, rewilding aims became broader, focusing on other ecological dynamics besides top–down control mechanisms, such as the reintroduction of large herbivores to maintain heterogeneous and open habitats (Carver et al., 2021). Before the global or local extinction of most of the largest herbivores and carnivores and before the replacement of wild herbivores by domesticated grazers, European landscapes were most likely characterized as a mosaic of forest, grassland and scrubland (Bullock, 2009; Johnson, 2009; Vera, 2000). The structural diversity of these landscapes was maintained by grazing of large herbivores and by fire (Sandom et al., 2014; Svenning, 2002; Vera, 2009).

The presence of large-bodied species at the end of the Pleistocene was associated with high diversity in vegetation structure (Sandom et al., 2014). In the early Holocene, large herbivores became less abundant and the prevalence of woodlands increased (Sandom et al., 2014). The pre-agrarian conditions found in the early to mid-Holocene have often been used as a benchmark in European rewilding efforts (Monsarrat & Svenning, 2022), focusing mainly on the reintroduction of large herbivores, with the goal of restoring ecological dynamics and promoting self-regulating ecosystems (Keulartz, 2016; Svenning et al., 2016). While rewilding programmes have been running for multiple years, monitoring of the effects of reintroductions on ecosystem dynamics remains complex, partially since most rewilding projects are open-ended (Lorimer et al., 2015). Nevertheless, the reintroduction of large herbivores (e.g. Highland and Tauros cattle) has shown to change vegetation structure and increase plant species richness (Garrido et al., 2019; Stroh et al., 2021).

These effects have also been associated with increased numbers of pollinators (Garrido et al., 2019; Konvička et al., 2021). Furthermore, European bison has been found to forage more in meadows compared to other ungulates, creating a greater impact on tree seedling growth, hence limiting tree encroachment (Kowalczyk et al., 2021). However, all effects from large herbivore reintroductions varied between sites and with reintroduced species.

One fundamental, remaining question in this context is whether trophic rewilding can restore ecosystems to their initial state (i.e. baseline state) or whether it results in conversion to a novel ecosystem (Corlett, 2016b). Conservation science and restoration ecology have now embraced the non-equilibrium paradigm (Botkin, 1990), which recognizes that ecosystems are often in a non-equilibrium dynamic, and ecological disturbances can move the system between multiple semi-stable states (Briske et al., 2020). The available evidence from reintroduction programmes is still sparse and hardly generalizable. Studies primarily focus on vegetation communities, limiting our understanding of how trophic rewilding influences ecosystem dynamics (Rubenstein & Rubenstein, 2016). The fact that most rewilding programmes are open-ended (Lorimer et al., 2015), the large spatial scales (e.g. thousands of square kilometres) and large temporal scales (e.g. hundreds of years), at which the involved ecosystem dynamics operate, make it hard to investigate the long-term consequences of rewilding approaches (Brown & Maurer, 1989; Nogués-Bravo et al., 2016; Root-Bernstein et al., 2018).

One promising approach to overcome these limitations and investigate the possible outcomes of rewilding actions is through the use of mechanistic ecosystem models (Enquist et al., 2020; Hoeks et al., 2020). These process-based models allow the exploration of alternative scenarios given specific actions and conditions, providing insights into the possible consequences of perturbations of complex systems over large spatial and temporal scales. Thereby, mechanistic ecosystem models may overcome common spatial and temporal limitations of empirical studies (Enquist et al., 2020; Newbold et al., 2020). The Madingley model (Harfoot et al., 2014) is a process-based general ecosystem model (GEM) that simulates a coherent ecosystem by modelling fundamental processes considering both autotrophic and heterotrophic life, relying on functional traits to determine the fate of organisms (Harfoot et al., 2014; Purves et al., 2013). It explicitly incorporates body size to regulate interactions between organisms, resulting in a body mass-structured food web, able to account for potential trophic cascading effects (Hoeks et al., 2020). By applying scenarios of change and focusing on emergent properties, it allows us to investigate the effects of specific events on ecosystem structure and functioning. The Madingley model explicitly simulates ecological interactions across multiple trophic levels and approximates individual-level dynamics, while not being limited by any specific set of species or environmental

conditions. As such, it provides the capacity to evaluate the potential outcomes of ecological pressures and restoration strategies targeting the degradation or reconstruction of ecosystem structure and functioning.

Here, we simulated the local extinction and reintroduction of large-bodied mammals in Europe using the Madingley model and assessed to what extent the ecosystem is brought back to the initial state. We focused our study on Europe, where trophic rewilding actions have taken place since 2011 in nine focal areas (https://rewildingeurope.com/areas/) and many other smaller localities (Pedersen et al., 2020; Root-Bernstein et al., 2018). These projects have primarily reintroduced or restocked populations of large herbivores (e.g. wild horses and bison) in order to promote the natural functioning of these ecosystems. Considering the focus on rewilding Europe, we limited our study to the effects of the removal and reintroduction of species existing within the body mass limits of a Holocene baseline. Besides the ongoing initiatives of rewilding Europe, narrowing down our simulations this particular context helps to make the results more comprehensive. Considering complexity of historical events observed across sites globally and between different baselines might make it harder to summarize the vast amount of results. We tested three different reintroduction scenarios, in order to disentangle the importance of the different large mammal groups (herbivores, carnivores and omnivores) and determine their role in restoring ecosystem processes and trophic structure. Since primary productivity and its seasonal pattern can influence ecological dynamics and the equilibrium state (Hoeks et al., 2020; Legagneux et al., 2014; Newbold et al., 2020), we repeated the simulation across four locations in Europe characterized by distinct levels of productivity and seasonality, to assess whether the recovery success depends on local environmental conditions. Since our goal was to examine the community's capacity to reestablish the original equilibrium considering spatial differences in environmental conditions, we assumed the selected study locations to be free of human pressures, such as the effects of land use (e.g. Newbold et al., 2017, 2020), in order to avoid unnecessary complexity. Similarly, we assumed climate conditions to be stable over time.

2 | METHODS

2.1 | Study areas

We selected four study areas in continental Europe differing in net primary productivity (denoted as NPP) and NPP seasonality, quantified by the yearly variation (standard deviation) in NPP. The four locations were selected by fitting a PCA on NPP and NPP seasonality variables and finding values that fall <0.25 and >0.75 of the quantiles of the first and second components. The Madingley model uses the grid cell-specific annual average temperature and annual total precipitation to estimate the grid cell's total annual NPP following the Miami model (Lieth, 1975). The annual NPP values are then divided into monthly fractions using a seasonality factor, calculated from external monthly NPP input data derived from remote sensing data (NASA, 2014); see assumption table 5 from Harfoot et al. (2014). The estimated monthly NPP values acquired from this procedure were used for the PCA analysis. This led to the identification of four sets of cells representing the extremes along the productivity and seasonality axes (see Figure 1). From each resulting subset of longitudes and latitudes identified by the PCA, a random location was sampled. The random sampling was confined to a minimum convex polygon with an isopleth of 50%. The isopleth was set to 50% in order to locate clusters of locations with similar conditions and avoid selecting isolated locations. Based on this approach, the simulation sites were selected in the following countries: France, Belarus, Spain and Norway (Figure 1).
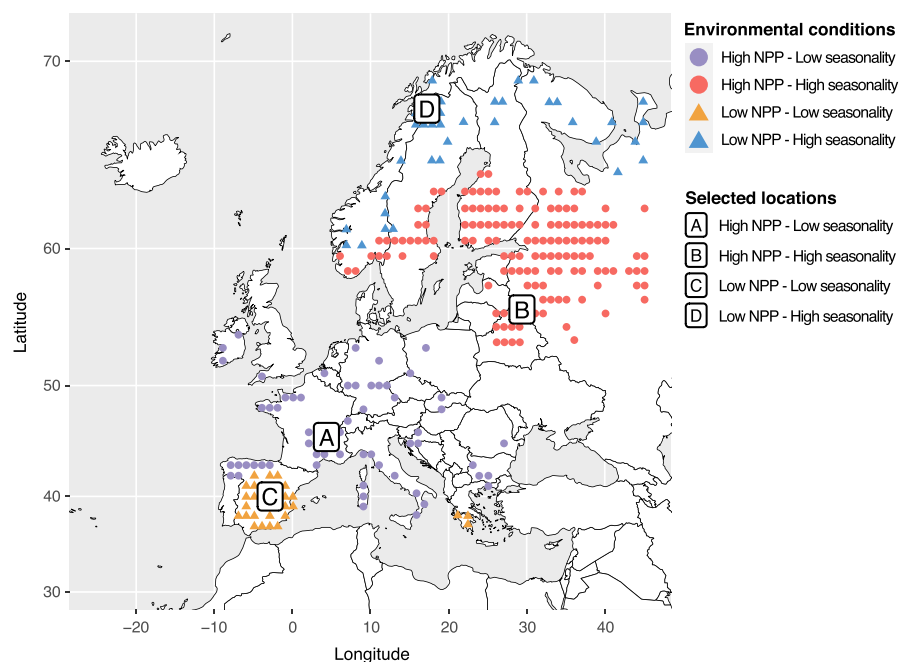
FIGURE 1 Selection of four simulation locations in Europe based on distinctive environmental conditions. Coloured dots show four opposing sets of environmental conditions based on the top quartiles of the two components of a PCA fitted on yearly average net primary productivity (NPP) and seasonality (quantified by the yearly standard deviation in NPP). The labels A to D show final geographic locations selected for the simulation runs.

For each location, an area of 6 by 6 spatial grid cells with a resolution of 0.5° (~3000 km^2) centred on the selected coordinate was used to run the simulations.

2.2 | Madingley model description

The Madingley model is a general ecosystem model (GEM) that aims to simulate ecosystems as a whole without being limited to a specific location, biome or subset of species (Harfoot et al., 2014). The main concept behind the functioning of GEMs is to reduce complex ecological processes to a set of core mechanisms that are applicable universally. In the context of the Madingley model, this is realized through the use of allometric scaling (Peters & Peters, 1986), individual-level traits and core ecological rules. The Madingley model simulates both photo-autotrophic and heterotrophic life and can be classified as an agent-based model, in which each agent represents a cohort of multiple individuals with similar categorical (e.g. thermoregulation strategy; diet category, reproduction strategy) and quantitative traits (e.g. adult body mass). Grouping individuals into cohorts, also referred to as super-agents, is done to reduce complexity and make large-scale simulations computationally feasible (Grimm & Railsback, 2013; Parry & Bithell, 2012). The main advantage of the agent-based approach applied by the Madingley model follows from the estimation of agent-level demographics and life history rates, as well as community-level characteristics such as trophic balance, which are not defined as model inputs, but follow from the included mechanisms (Harfoot et al., 2014). The combination of the functional traits of a cohort, general allometric relationships, local environmental conditions, autotrophic biomass and the status of other cohorts within the same spatial grid cell determines the actions of each cohort at a given time step in the simulation. These actions include, for example, metabolizing, feeding on autotrophs, predating on other cohorts, reproducing and moving to other spatial grid cells (Harfoot et al., 2014). The autotrophs are modelled as a function of the environmental conditions using a terrestrial carbon model (Smith et al., 2013). The model's emergent properties are thereby dictated by local-scale ecological processes and environmental conditions, rather than follow from empirical extrapolations, often outside the scope of the original input data (Wüest et al., 2020). As such, models such as Madingley may respond more appropriately to novel conditions and allow for the exploration of a multitude of scenarios using simulation experiments. In addition, they enable estimations of a wide range of ecologically relevant parameters across large temporal and spatial scales. An in-depth description of the model and its mechanisms can be found in the original publication of the model (Harfoot et al., 2014).

2.3 | Rewilding simulation setup

We ran the simulation using the R package of the Madingley model, that is MadingleyR (Hoeks et al., 2021). Besides the additional functionality of MadingleyR useful in our simulations (e.g. model restarts and logging cohort interactions), the MadingleyR package used for these simulations also includes the updated predator–prey body mass interactions. This update allows large carnivores to hunt on larger prey species following the threshold observed by Carbone et al. (1999). Two modifications were implemented to the standard code of the MadingleyR package in order to improve the realism of the simulations: (1) the competition for resources between herbivore body mass categories was partially lifted by binning herbivores into 8 bins and allowing each bin to feed on independent vegetation stocks, and (2) small-bodied prey (<150 g) were made invisible to predators once the summed cohort density of all cohorts with similar traits dropped below a set threshold of <1 individual per km^2 to protect them from going extinct. This is a highly conservative assumption, as small mammals generally occur at high densities (Santini et al., 2022). Both modifications are described in detail in Appendix S1. Our simulations exclude any pressures of humans, as such, we did not include the human appropriation of net primary productivity previously studied using the Madingley model (e.g. Newbold et al., 2017, 2020).

The simulation followed three main steps: (1) seeding the model and creating the initial (pristine) state; (2) removing all large-bodied mammal groups (>200 kg herbivores; >100 kg omnivores; and >10 kg carnivores), resulting in the post-removal model state; and (3) reintroducing of large-bodied mammal groups, resulting in the post-reintroduction model state (Figure 2). At the end of each of these steps, the simulation was given time to stabilize (Figure 2).

The Madingley model was initialized using the default model parameters, cohort definitions and stock definitions. For all locations, we seeded the model with the same cohort definitions using a maximum body mass of 700 kg for endothermic herbivores (e.g. bison and auroch), 200 kg for endothermic omnivores (e.g. matching European populations of brown bear) and 50 kg for endothermic carnivores (e.g. grey wolves) (Crees et al., 2016); see Table S1 for cohort definitions. These maximum body mass values represent a Holocene baseline (Crees et al., 2016), a state that could be easily recoverable by focusing on the reintroduction of large-bodied mammals to regions where they have been lost. Nevertheless, in the Holocene many natural functions and processes were already lost due to the absence of the even larger, megafauna species (Ellis et al., 2021; Larson & Fuller, 2014; Sandom et al., 2014; Schowanek et al., 2021). The roles of these megafauna species, with body masses >1000 kg for herbivores and >100 kg for carnivores (Malhi et al., 2016), are not considered in our simulation experiment. After the initialization procedure, we run the model for 1000 years in order to reach stable equilibria. The state at the end of this spin-up phase, from here on referred to as the initial state, was exported and used as the control in our analysis (see Figure 2, step 1).

In the removal phase, we removed one cohort per trophic group per year until all cohorts above a predetermined body mass threshold have gone extinct. Cohorts selected for removal were sorted by adult body mass, removing the largest bodied cohorts first. We used the following thresholds to define and remove large mammals
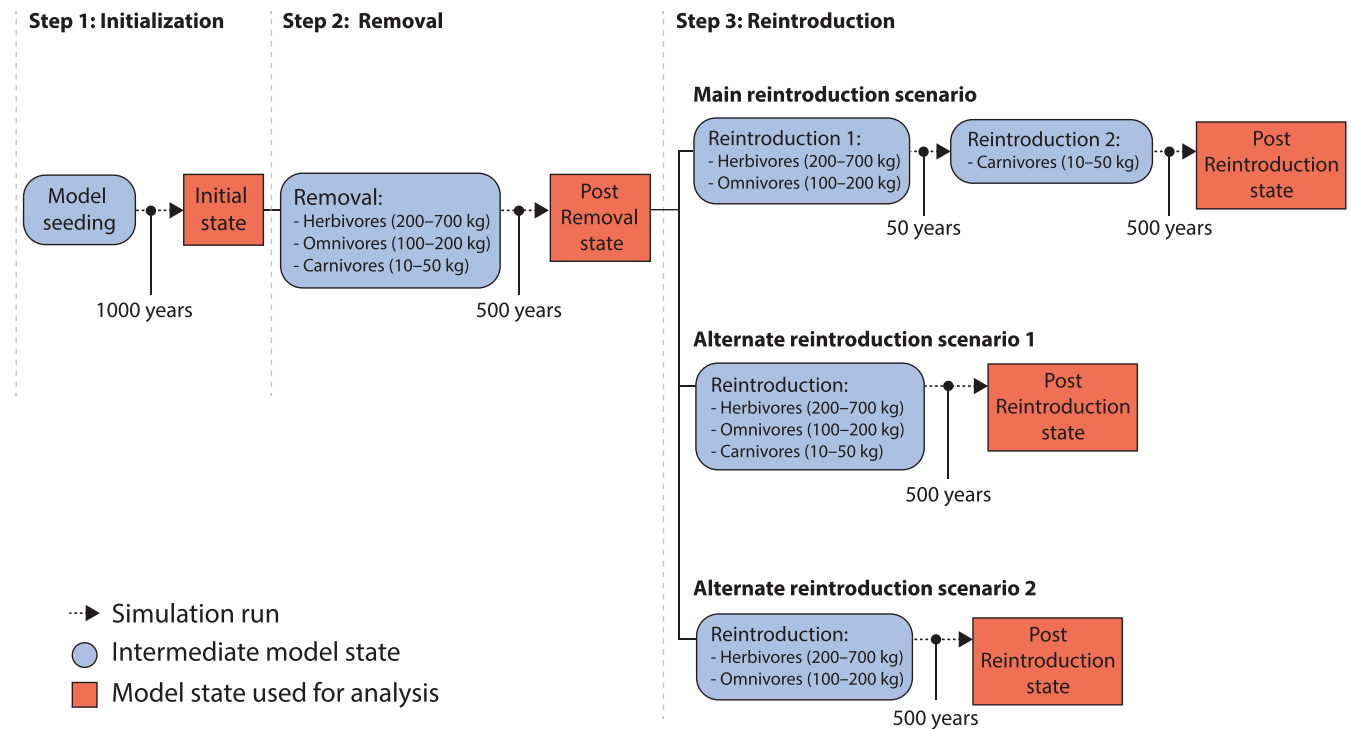
FIGURE 2 Simulation overview. Illustration shows how the consecutive model states are linked, the various simulation durations and differences between the reintroduction scenarios (step 3). The entire simulation procedure as shown here was applied 10 times for each location, resulting in 10 post-reintroduction replicates per location and per reintroduction scenario.

for all European locations: (1) large herbivores >200 kg (~ size of a red deer); (2) large omnivores >100 kg (~size of a wild boar); and (3) large carnivores >10 kg (retaining mesopredators). Following the removal phase, the model was run for another 500 years to reach a new stable equilibrium. The end of these 500 years (post-removal state) was saved for the continuation of the simulation experiment (see Figure 2, step 2).

The main reintroduction scenario was conceived to replicate existing trophic rewilding projects, where the focus lies on restoring grazing regimes by reintroducing large herbivores (Vera, 2009), under the assumption that carnivores naturally recolonize the area once prey are sufficient and disturbance is reduced (Cimatti et al., 2021). This main scenario was started from the post-removal equilibrium state. In this step of the simulation, large herbivore and large omnivore cohorts were reinserted with yearly intervals, starting from the lightest bodied cohort and working up to the heaviest bodied cohort. After the herbivore and omnivore reintroduction phase, we let the model stabilize over a period of 50 years, after which we started with the reintroduction of large carnivores, again starting with the lightest bodied cohort and working up to the heaviest. Before inserting cohorts back into the simulation, we first aggregate the previously removed cohorts by functional groups and body mass to reduce the number of reintroductions. Additionally, we set the abundance of the cohorts to reinsert to 10 individuals per cohort. After the completion of both phases, we let the model run for another 500 years and exported the post-reintroduction state (see Figure 2, step 3).

Alongside the main reintroduction scenario, we designed two alternative reintroduction scenarios to disentangle the importance of the different large mammal groups (herbivores, carnivores and omnivores) in restoring ecosystem processes and trophic structure. In the main reintroduction scenario, large herbivores and omnivores were reintroduced first followed by a delayed reintroduction of large carnivores. The first alternative reintroduction scenario reintroduces large herbivores, large omnivores and large carnivores with yearly intervals during one single phase. This scenario simulates a case in which the three functional groups are reintroduced simultaneously. The second alternative reintroduction scenario only reintroduces large herbivores and omnivores without large carnivores. The underlying idea of this reintroduction scenario was that natural recolonization by large carnivores is not always possible due to, for example, the size and connectivity of the rewilding site (Santini et al., 2016) or societal opinions around the reintroduction of large carnivores (Chandelier et al., 2018; Figari & Skogen, 2011; López-Bao et al., 2017). Figure 2 provides an overview of the main reintroduction scenario and the two alternative reintroduction scenarios.

2.4 | Post-processing

When analysing the simulation outputs, we focused on the distribution of endothermic biomass across different functional groups in the ecosystem. For this purpose, endothermic biomass was

aggregated into seven different categories: all endotherms, herbivores (body mass < 200 kg), carnivores (body mass <10 kg), omnivores (body mass <100 kg), large herbivores (body mass >200 kg), large carnivores (body mass >10 kg) and large omnivores (body mass >100 kg). In addition to the biomass of the endothermic categories, we also considered the response in autotroph biomass. Relative differences were calculated for each category between the initial state and the post-removal state (post-removal/initial), and between the initial state and the post-reintroduction state (post-reintroduction/initial), to quantify the shifts in biomass following the simulation events. All results presented in this study represent averages over the last 5 years of a specific simulation phase across 10 replicates. The standard deviation was calculated to show the variation between simulation replicates.

We estimated the overall difference in maximum trait space volume of the initial state and the post-reintroduction state of the same community using the Jaccard dissimilarity index. This index describes beta-diversity and is computed based on the relative positioning of the convex hulls of two community assemblages. In this study, trait space was comprised of log_{10} adult body mass, trophic index, and functional group index (see Table S1) using the *mFD* package (Magneville et al., 2022). The dissimilarity in trait space was calculated as the average Jaccard index of 5 samples of 10,000 cohorts for each location–reintroduction–replicate combination, where the variation in Jaccard index represents the variation between replicates.

We also used the Jaccard dissimilarity index to quantify differences in the distribution of biomass within the same community between the initial state and the post-reintroduction state. Because the Madingley model follows a trait-based approach (i.e. does not model species) and traits are modelled on a continuous scale, grouping cohorts into larger aggregates is required for the comparison of two communities using the regular Jaccard index. Here, we aggregated the biomass of cohorts using log_{10} body mass bins and functional group (see Table S1). The resulting bins were used to calculate the Jaccard index using the 'vegdist' function of the *vegan* package (Oksanen et al., 2007). The body mass bins were sufficiently coarse to avoid overestimation of the Jaccard index caused by changes in cohort body mass during the simulation, for example due to merging of cohorts at each time step (Harfoot et al., 2014). Figure S1 shows the sensitivity of the selected bin width on the computed Jaccard dissimilarity index. The log_{10} body mass bins match with our main groups of interest (e.g. large-bodied herbivores between ~100 and 1000 kg, medium-sized herbivores ~10 and 100 kg; large carnivores between 10 and 100 kg; mesopredators between 1 and 10 kg; and large omnivores between 100 and 1000 kg). The computed Jaccard index of the body mass distribution therefore quantifies macroscopic differences in community structure between the initial state and the post-reintroduction state. Similar to the dissimilarity in trait space, the dissimilarity in body mass distribution was calculated for each location–reintroduction–replicate combination and averaged per location–reintroduction scenario where the variation presented in the paper indicates the differences between replicates.

Finally, we applied a variance decomposition analysis to quantify how different reintroduction scenarios and differences in local environmental conditions contributed to the simulation outcome. The simulation outcomes were summarized using the response ratio. The response ratio was calculated by taking the natural logarithm of the biomass post-reintroduction divided by the biomass of the initial state. Response ratios were calculated for each of the following eight biomass aggregates: all autotrophs, all endotherms, herbivores <200 kg, omnivores <100 kg, carnivores <10 kg, herbivores >200 kg, omnivores >100 kg and carnivores >10 kg (see Figures 3–5), resulting in eight response ratios per simulation. We performed one ANOVA per response ratio to derive the sum of squares for the reintroduction scenario, the local environmental conditions and the residuals. These were then divided by the total sum of squares, resulting in the variance attributable to each of these factors. The variance decomposition analysis included the results of 10 simulation replicates per unique combination of reintroduction scenarios (three scenarios) and local environmental conditions (four locations), resulting in 120 inputs per ANOVA model.

3 | RESULTS

We first present the results of the removal of large mammals; these are simulated using an identical approach across all subsequent reintroduction scenarios. Next, we describe the main reintroduction scenario, in which large herbivores and omnivores are reintroduced first, followed by a delayed reintroduction of large carnivores. After that, the two alternative reintroduction scenarios are compared with the main scenario.

3.1 | Removal of large mammals

Our simulation results showed that endothermic herbivores <200 kg and omnivores <100 kg increased in overall biomass across all locations following the removal of large-bodied endotherms (see Figure 3; Figure S2). This observation stems from a reduced competition for resources due to the removal of large herbivores (>200 kg) and a loss of top–down control due to the removal of large carnivores (>10 kg). Observed increases in endothermic herbivore (<200 kg) biomass were stronger for locations characterized by low seasonality (low productivity = 72% ± 8% and high productivity = 88 ± 13%) compared to locations with high seasonality (low productivity = 38% ± 6% and high productivity = 46% ± 9%). Although less pronounced, endothermic omnivore (<100 kg) biomass increases showed the opposite trend, with larger increases in locations with high seasonality (low productivity = 28% ± 10% and high productivity = 29% ± 9%), compared to increases observed in locations with low seasonality (low productivity = 21% ± 10% and high productivity = 14% ± 11%). Across all four locations, the removal of large mammals resulted in a minor decrease in available autotroph biomass (Figure 3).
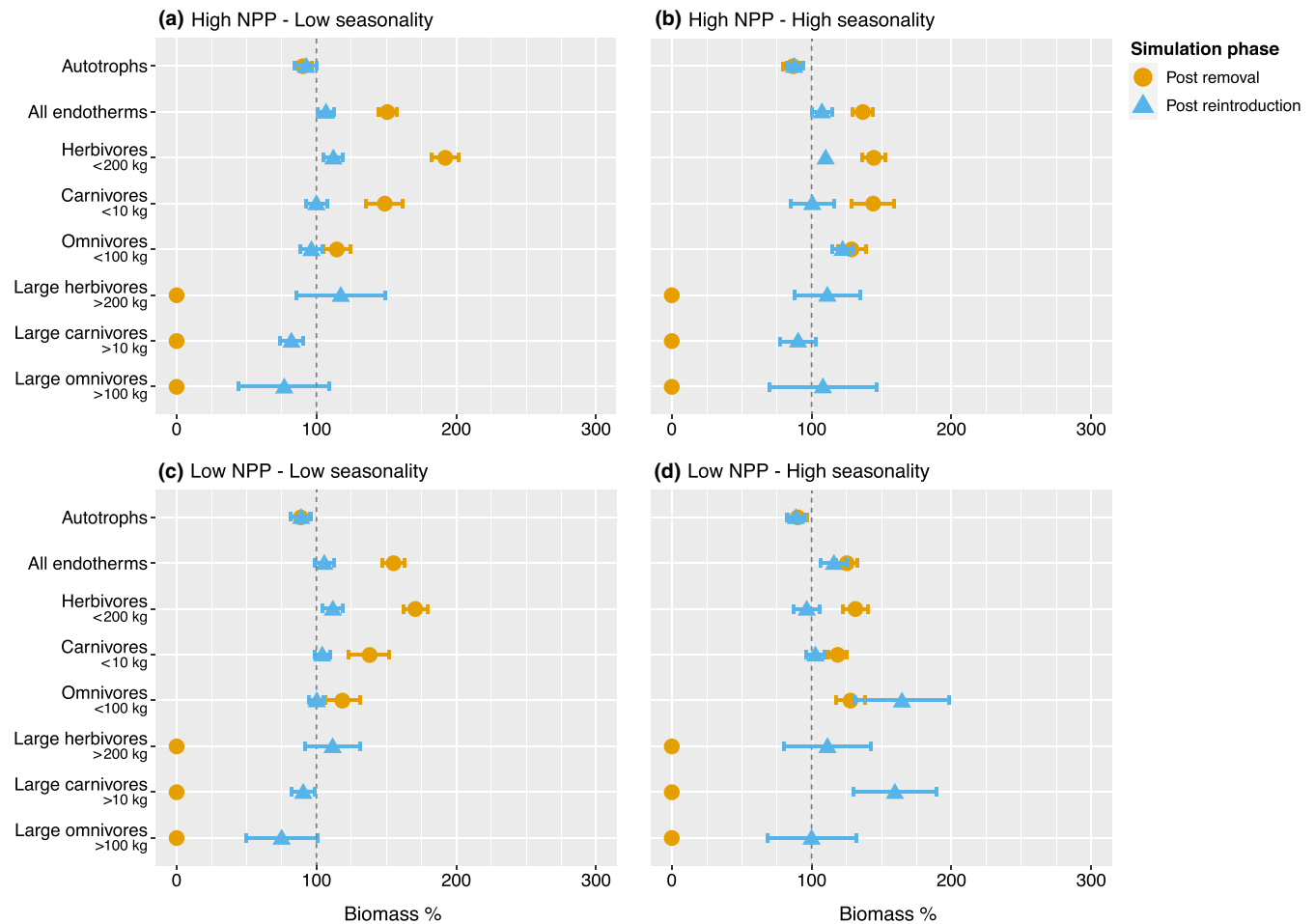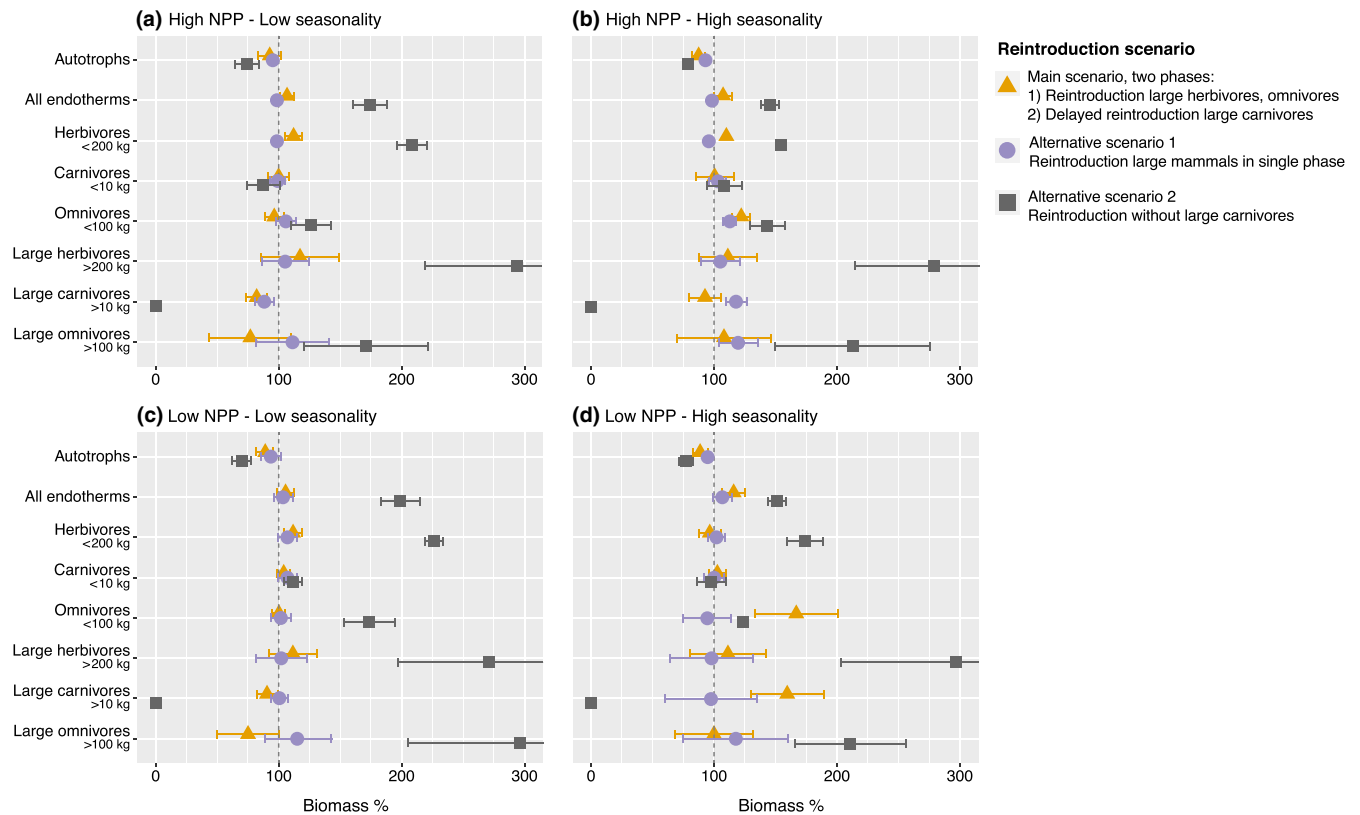
FIGURE 3 Shifts in equilibria across four locations in Europe (a-d) following the removal and reintroduction of large mammals. Endothermic large-bodied cohorts (large herbivores >200 kg; large carnivores >10 kg; and large omnivores >100 kg) were removed from the initial state, starting with the heaviest animals. After the model reached an equilibrium, large herbivores and large omnivores were reintroduced first, followed by the reintroduction of large carnivores. Orange dots depict the relative change in biomass after the removal event compared to the initial state, and blue triangles show the relative change in biomass compared to the initial state after the reintroduction events. Relative changes in the biomass for each of the group and each model phase are expressed as percentages of the initial (pre-removal) biomass, depicted by the vertical dashed lines (e.g. 100% indicates no change in biomass; 0% indicates none of the biomass of the initial state is retained; and 200% shows a doubling of the biomass of the initial state). Changes in biomass are based on yearly averages calculated over the last 5 years of each specific simulation phase and across 10 replicates. Bars show the standard deviation between the averages of 10 replicates.

Carnivores <10 kg (mesopredators) increased in all four locations (Figure 3; Figure S2) following the loss of top–down control exerted by larger (>10 kg) carnivores and because of increased prey availability. This result was more pronounced in locations characterized by high productivity (low seasonality = 48% ± 13% and high seasonality = 45% ± 14%), compared to low-productive locations (low seasonality = 37% ± 14% and high seasonality = 21% ± 5%).

3.2 | Reintroduction of large mammals

Across all four locations, the simulation outcomes showed an increase in autotroph biomass and a decrease in biomass of small endotherms when comparing the post-reintroduction state to the post-removal state (Figure 3). These biomass changes following the reintroduction of large mammals indicate a shift towards the biomasses found in the initial state. However, the biomass of large herbivores was slightly greater after the reintroduction event compared to the initial state (Figure 3). We also found that in highly seasonal and low-productive locations, the system's ability to return to an equilibrium close to that of the initial state is lower, compared to more stable and productive systems. In the high-seasonality locations, the biomass of smaller-sized endothermic omnivores remained larger after the reintroduction compared to the initial state (see Figure 3b,d). Large carnivore biomass increased after the reintroduction compared to the initial state in the high-seasonality and low-productivity locations, following the relative increase in preferred prey biomass (smaller-sized omnivores).

FIGURE 4 Shifts in equilibria compared to the initial state following three different large mammal reintroduction scenarios across four locations in Europe (a–d). Orange triangles depict the relative biomass compared to the initial state for the main reintroduction scenario, which reintroduces large herbivores (>200 kg) and large omnivores (>100 kg) first, followed by a delayed reintroduction of large carnivores (>10 kg); purple circles show the relative biomass following the reintroduction of all large-bodied groups within the same simulation phase (alternative reintroduction scenario 1); and grey squares show the relative biomass compared to the initial state resulting from the reintroduction of large herbivores and large omnivores only (alternative reintroduction scenario 2). Relative changes in the biomass for each of the group and each model phase are expressed as percentages of the initial (pre-removal) biomass, depicted by the vertical dashed lines. Computed changes in biomass equilibria are based on yearly averages computed over the last 5 years and across 10 replicates.

3.3 | Trait-based community dissimilarity

We quantified the differences in the maximum trait space volume of the initial state and the post-reintroduction state using the Jaccard dissimilarity index and found a difference of 9.1% on average over all locations for the main reintroduction scenario (Table S2). The Jaccard dissimilarity is the sum of two factors: (1) the turnover in community trait composition, that is the replacement of functional trait combinations from site to site (Baselga, 2010), and (2) nestedness, that is differences in trait composition resulting from net loss of trait combinations (Baeten et al., 2012). For locations with high seasonality, the trait space dissimilarity was mostly comprised of nestedness (0.5%–1.2% turnover and 7.9%–8.1% nestedness), suggesting that the post-reintroduction state had a smaller trait space and almost no new trait combinations were found. For locations with low seasonality, the trait space dissimilarity was comprised equally of turnover and nestedness in community trait composition (3.7%–5.1% turnover and 4.7%–5.2% nestedness), suggesting that the initial state and the post-reintroduction state fill a similar trait space volume.

3.4 | Body mass distribution dissimilarity

We also used the Jaccard index to quantify differences in $\log_{10}$-binned body mass distributions within functional groups between the initial state and the post-reintroduction state. On average, the dissimilarity between the binned body mass distribution was 28% for the main reintroduction scenario indicating a substantial restructuring of biomass distribution across organisms under all simulated environmental conditions (see Figure S3). The Jaccard index did not substantially differ between the locations (see Table S3), suggesting similar amounts of change within the biomass distribution yet different body mass bins increase or decrease in abundance among the locations.

3.5 | Comparing reintroduction scenarios

The reintroduction of large herbivores and omnivores followed by the delayed reintroduction of large carnivores (main reintroduction scenario) shifted the equilibrium of endotherm biomass distribution back to a state closely resembling the initial conditions (Figure 4). The
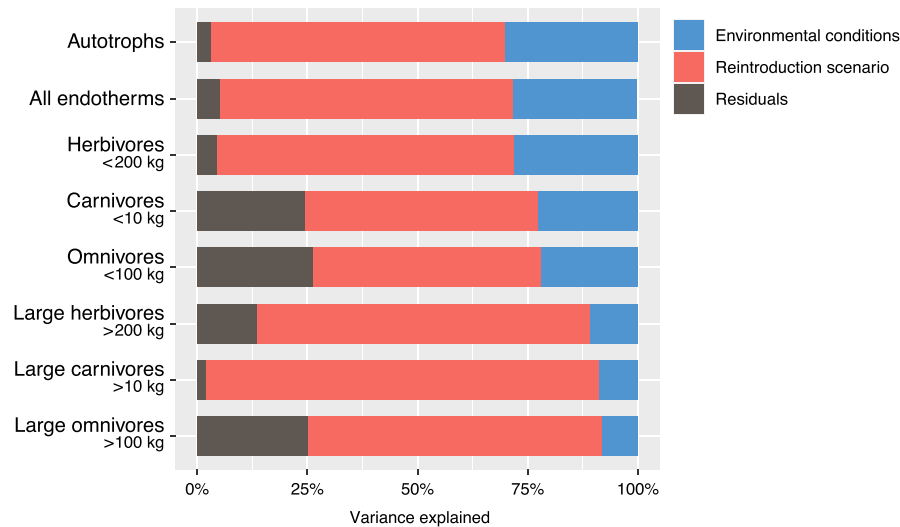
FIGURE 5 Variance decomposition analysis. Contribution of local environmental conditions and different reintroduction scenarios to the variance in simulated response ratios. The response ratio was calculated by taking the natural logarithm of the biomass in the post-reintroduction state divided by the biomass in the initial state. Body mass thresholds for characterizing cohorts as large are the following: large herbivores >200 kg; large carnivores >10 kg; and large omnivores >100 kg. Biomass inputs used to derive the response ratios were based on yearly averages computed over the last 5 years of the simulation phase. The variance explained was calculated using an ANOVA, in which the sum of squares for the reintroduction scenario, the local environmental conditions and the residuals was divided by the total sum of squares. The variance decomposition analysis includes results from 10 simulation replicates per unique combination of reintroduction scenarios and local environmental conditions.

reintroduction of large herbivores, large omnivores and large carnivores in one single simulation phase (alternative scenario 1) shifted the biomass distributions closest to those found in the initial state (Figure 4). In this scenario, large carnivores were able to exert a top–down control on herbivores and omnivores from the moment they were reintroduced, thereby reducing the abundance of herbivores and limiting the impact on autotroph biomass. Although the simultaneous reintroduction of large herbivores, omnivores and carnivores (alternative scenario 1) performed best in terms of restoring biomass distributions when considering the average biomass over multiple simulation replicates (purple circles, Figure 4), the variation between simulation replicates remained large (purple error bars, Figure 4). This large variation indicates that the recovery performance varied widely across individual simulation runs, while on average (out of 10 replicates) recovery success is expected to be high. This observation especially holds for low-productive and highly seasonal locations (Figure 4d). The reintroduction scenario, which did not reintroduce large carnivores at all (alternative scenario 2), ranked the lowest in terms of restoring the biomass distribution of the other endothermic groups to their initial states, with large shifts in the equilibrium after the reintroduction event (see Figure 4).

The scenario in which large-bodied carnivores were not reintroduced showed the highest community dissimilarity in maximum trait space volume (location average: 13.7%; see Table S2), where the higher nestedness compared to turnover for all locations except the high-productivity and low-seasonality location, suggests a smaller trait space for the post-reintroduction state (see Table S2). Similarly, the scenario without large-bodied carnivore reintroduction showed the highest community dissimilarity in $\log_{10}$ binned biomass

distribution (location average: 37.1%; see Table S3) when comparing the initial state to the post-reintroduction state. The dissimilarity in maximum trait space volume between the initial state and the post-reintroduction state was similar for the main reintroduction scenario (with delayed large carnivore reintroduction) and the scenario that reintroduces all large-bodied mammals simultaneously (see Tables S2 and S3). However, the biomass distribution dissimilarity for the scenario that reintroduces all large-bodied mammals simultaneously was smaller (location average: 22%; see Table S3) compared to the biomass distribution dissimilarity found for the main reintroduction scenario (location average: 28%; see Table S3).

3.6 | Relative importance of reintroduction strategy and environmental context

Both the local environmental conditions and the reintroduction scenario influenced the outcome of the reintroductions (Figure 5). The reintroduction scenario was the most important determinant for the differences in biomass between the initial state and the post-reintroduction state for all groups with an explained variance between 54% and 88%. The environmental conditions also played a role in determining the biomass of herbivores, carnivores, omnivores and autotrophs (21%–32%), but appeared to be of lesser importance to the large herbivore, large carnivore and large omnivore groups (7%–12%).

When excluding the results of the second alternative reintroduction scenario, the importance of the reintroduction scenario in explaining the variation between runs decreased (Figure S4). Overall, the unexplained variation due to model stochasticity (i.e. residual

variation) increased, and for large-bodied mammals, the environmental conditions played a more important role in explaining the variation in simulation outputs (Figure S4).

4 | DISCUSSION

4.1 | Large-bodied mammal removal

To assess different rewilding strategies in terms of their ability to restore the original trophic structure, we first simulated the extinction of large-bodied mammals in Europe under different environmental conditions. The extinction of large-bodied mammals led to large cascading effects on smaller-bodied mammal biomass and autotroph biomass, with an overall increase in endotherm biomass. According to our simulations, the magnitude of these shifts in ecosystem structure depended on the productivity and seasonality of the ecosystem, with larger changes in systems with low seasonality (see Figure 3).

Our simulation results further show that small-sized and medium-sized (<10 kg) carnivore biomass increased after the removal of large-bodied mammals, especially under high-productive conditions, thereby supporting the 'mesopredator release hypothesis' (Soulé et al., 1988; Terborgh & Winter, 1980). Examples in Europe of this are the expansion of the golden jackal, which has been proposed to have resulted from the widespread decline of the wolf (Krofel et al., 2017), as well as the suppression of the red fox abundance where the Eurasian lynx is present (Pasanen-Mortensen et al., 2013). The simulation results obtained by Enquist et al. (2020) showed that the removal of large herbivores (>100 kg) disproportionately lowers the productivity of ecosystems on a global scale. In many ways, these simulations are comparable to ours. However, the combined removal of large herbivores (>200 kg), large carnivores (>10 kg) and large omnivores (>100 kg) implied a strong restructuring of the endothermic biomass distributions as a result of trophic cascades (see Figure 3, Figure S2). For example, the loss of large carnivores directly released medium-sized (e.g. 10–200 kg) herbivores for top–down control, allowing for increases in mesopredator biomass.

In line with our findings, experimental exclusion studies have shown that the abundance of small-bodied mammal species increases when large herbivores are absent (Keesing, 1998; Long et al., 2017; Young et al., 2015). In our simulation results, this observation stems from a decrease in and loss of predation. Besides the competition for resources or changes in food quality (Hagenah et al., 2009; Keesing, 1998), the field studies identified a change in the composition of plant communities following the exclusion of large herbivores, propagating to suppress small mammals by altering their behaviour (Long et al., 2017).

4.2 | Large-bodied mammal reintroduction

Overall, our simulations suggest that the shifts in ecosystem structure, resulting from the large-bodied mammal removal, can be partially turned around and restored to a state resembling the baseline ecosystem following the reintroduction of large-bodied mammals (Figure 3). The recovery success in the simulated locations characterized by low productivity and high seasonality showed to be the lowest, suggesting that the restoration of ecosystem structure and functioning might be more challenging for these sites. This finding also suggests that the outcomes of rewilding initiatives are likely not always generalizable.

Our simulations also indicate that reintroducing large carnivores together with large herbivores and large omnivores may increase the recovery performance, resulting in final biomasses closer to the initial state (see Figure 4). This finding indicates that deciding to actively reintroduce carnivores, or allowing them to recover naturally, can have important consequences on the end state of an ecosystem, as herbivores have the time to alter the system substantially before carnivores are present. Consistent with this line of reasoning, the recovery of biomass distributions to the initial state was lowest in the reintroduction scenario that assumed no return of large carnivores (Figure 4). The results related to this scenario showed strong increases in endothermic biomass and decreases in autotroph biomass. These results align with previous simulation experiments and empirical investigations looking into the importance of top–down regulating mechanisms exerted by large carnivores (Estes et al., 2011; Hoeks et al., 2020), and they support the 'green world hypothesis' (Bond, 2005; Wilkinson & Sherratt, 2016).

Losing top–down control in ecosystems can, however, be compensated by the continued presence of humans (Darimont et al., 2015), replacing the function of large carnivores by harvesting herbivore biomass. Nevertheless, this may lead to unnatural population reductions or losses of the herbivore species (Malhi et al., 2016; Ripple et al., 2015). Moreover, the continued involvement of humans is against rewilding principles, whose goal is to restore self-regulating property of ecosystems by recovering natural dynamics (Carver et al., 2021; Corlett, 2016b; Lundgren et al., 2018).

The simulations conducted with the Madingley model suggest that rewilding actions can restore ecosystem processes and recover trophic structure such that it closely resembles the baseline, to an extent that depends on the reintroduction scenario and the environmental conditions (see Figure 5). However, even in a simplified simulation experiment characterized by consistent differences in environmental conditions and a structured reintroduction protocol, the simulated system does not always stabilize to a state that is equal to the initial state in terms of trophic structure, for example ~65% increase in biomass of omnivores and a ~60% increase in biomass of large carnivores in locations with low productivity and high seasonality or a ~20% decrease in the biomass of large carnivores in locations with high productivity and low seasonality (see Figure 3). Across all locations, we observed a decrease in autotroph biomass and an increase in overall endothermic biomass (see Figure 3). We also observed increases in large herbivore biomass across all locations, suggesting that gradual recovery of large carnivores in the main reintroduction scenario led to a community in which large herbivores are more abundant compared to the baseline (Le Roux et al., 2019).

Moreover, differences in the maximum trait space (quantified by the Jaccard community dissimilarity; see Table S2) and differences in the biomass distribution suggest a restructuring of the ecosystem.

4.3 | Simulation considerations

An important goal of rewilding is to create open and diverse landscapes by reintroducing grazers (Pereira & Navarro, 2015). We are currently not able to test changes in the landscape configuration with the Madingley model, as it only provides changes in vegetation (autotroph) biomass (Harfoot et al., 2014). Our results showed that, after the removal of large-bodied mammals, the biomass of smaller-bodied mammals increased (see Figure 3). In the simulation, this could be explained by decreased competition for plant biomass and loss of top–down control exerted by large carnivores. However, in the real world, the opposite has also been described, where the presence of large herbivores may increase the biomass of herbaceous and other low-growing plants due to the suppression of woody plant biomass (Bakker et al., 2016), leading to an increase in food availability to smaller organisms. The Madingley model currently only considers the growth of a consumable evergreen and deciduous pool of vegetation mass per grid cell. The absence of structured vegetation classes in Madingley makes it impossible to include vital animal–plant interactions able to capture these feedbacks. Moreover, defining vegetation on such a high level makes it currently impossible to consider differences in the nutritional content of food sources and assign animals into more detailed diet categories. As such, Madingley is as of yet not able to differentiate along the grazer–browser continuum (Lamprey, 1963) nor does it include the role of detritivores. As a result, it is impossible to study these types of structural changes, implying that our approach is incapable to capture feedbacks between changes in the community of animals and that of vegetation. Future model developments on the coupling of Madingley with LPJ-GUESS could enable the inclusion of more detailed animal–plant interactions (Krause et al., 2022). In addition to the absence of structured vegetation classes, the current modelling framework simulates the landscape in 2D; adding a third dimension would enable the model to further specify niche habitats for specific animal groups. This could allow future research to focus on how the introduction of large mammals might alter the 3D structure of the landscape and influence the availability of resources for other groups of animals, capturing in more detail the mechanisms discussed by Bakker et al. (2016).

Here, we have focused on the reintroduction of large-bodied mammals without considering the many challenges of reintroduction programmes, especially related to large omnivores (e.g. bears) or carnivores (e.g. wolves). We expect the reintroduction success to be higher in our simulations compared to real-life situations as we do not account for human impact, public responses and other practical challenges such as continuous conservation funding and conflict management (Stier et al., 2016). Moreover, the Madingley model follows a trait-based approach, heavily relying on allometric

scaling; as such, it is not capable of capturing species-specific interactions or requirements. Rewilding Europe is carrying out reintroductions, all of which focus on herbivores and omnivores, assuming carnivores will come back naturally. While this is a well-justified expectation (Chapron et al., 2014; Cimatti et al., 2021; Reinhardt et al., 2019), the time of recolonization would be unpredictable and recolonization itself cannot be taken for granted. For example, the natural recolonization by large carnivores is not always possible due to the size and connectivity of the rewilding site (Santini et al., 2016) or because of societal opinions surrounding the return of large carnivores (Chandelier et al., 2018; Figari & Skogen, 2011; López-Bao et al., 2017).

Finally, the restoration success could differ from real-life situations as a result of a wide range of external factors, such as temporal changes in climatic conditions, increases in human population density, the expansion of croplands and the release of invasive species. These factors were not included in our simulation framework. Empirical data have demonstrated how the site occupancy of European large-bodied mammals can vary between species as a result of variations in environmental and human-related covariates (Ament et al., 2023; Crees et al., 2016), potentially providing insights into the persistence of particular species following natural recolonization or active reintroduction considering local conditions. Subsequent scenarios could consider a wider range of environmental conditions, potential impacts of climate change and human-induced pressures following a systematic approach. Future research could further explore the possible outcomes of rewilding actions by including more comprehensive animal–vegetation feedbacks and investigating fine-scale ecosystem attributes.

4.4 | General conclusions

All in all, our simulation results point out that trophic rewilding holds great potential as a conservation tool and provides support to several principles in rewilding presented previously (Carver et al., 2021). For instance, our simulations show that natural patterns and dynamics of abundance and distribution can be partially restored and result in a self-sustaining ecosystem (Carver et al., 2021). Our reintroduction scenarios suggest that the reintroduction of large-bodied herbivores together with the reintroduction or natural recolonization of large-bodied carnivores is important to restore the full array of species required for successfully recovering an ecosystem to the baseline ecosystem, underlining the importance of landscape connectivity and public understanding (Bluhm et al., 2023; Boitani & Linnell, 2015; Carver et al., 2021).

While trophic rewilding can restore natural dynamics, our results support the notion that the resulting ecosystem may not necessarily resemble its original states (Corlett, 2016a) and outcomes are hard to anticipate for individual cases. Similar challenges have been discussed in the context of restoration efforts in general (Baumane et al., 2021; Higgs et al., 2014; Palmer et al., 2016; Suding et al., 2004, 2016). While this remains a debated point in the

rewilding community, several authors emphasized that the aim of rewilding projects is not to recover ecosystems to a historical baseline state, but rather to restore an ecosystem with high ecological complexity and high capacity for biodiversity (Perino et al., 2019; Svenning, 2020). The perceived unpredictability in the outcomes of rewilding actions has attracted criticisms by some researchers (Nogués-Bravo et al., 2016), and unarguably, rewilding approaches require a shift in conservation perspective as setting measurable objectives and anticipating changes may be challenging (Tear et al., 2005). Uncertainties can be partially removed by improved and novel monitoring programmes (Mata et al., 2021), assisting in the identification of undesirable trajectories (Prach et al., 2019).

The success of rewilding projects may be more meaningfully measured by focusing on the increases in ecological integrity and complexity (Bullock et al., 2022; Segar et al., 2022; Torres et al., 2018), irrespective of the hypothetical original (baseline) state. This is also relevant in the prospect of accelerated rates of climate change and wide variations in ecological rates of change, making it increasingly difficult to rely fixed target states for management strategies (Williams et al., 2021). Rewilding can play a key role in the conservation of the 21st century; however, it will be vital to carefully define the expected outcomes and provide sound methodologies for measuring the success of rewilding actions. Our study contributes to this discussion by showing that trophic rewilding can—broadly—restore the structure and processes of baseline ecosystems. Nonetheless, it also highlights shifts and uncertainties that need further attention.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The example simulation codes are available under: https://github.com/SHoeks/RewildMadingleyR

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.