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Rewilding Strategies in Semi-Arid Ecosystems

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ABSTRACT

Rewilding -- the passive or active restoration of ecological processes, trophic interactions, and species assemblages toward self-regulating ecosystem states -- is increasingly applied in semi-arid Mediterranean and sub-Mediterranean landscapes where agricultural abandonment, overgrazing legacy, and long-term predator depletion have created ecologically degraded but potentially restorable terrain. This study monitored biodiversity, vegetation structure, and ecosystem function responses across 42 rewilding sites in Spain, Portugal, and Greece representing three rewilding strategies -- passive rewilding (agricultural abandonment with no active management), large herbivore reintroduction (Bos taurus primitive breeds, Equus ferus caballus, Cervus elaphus), and apex predator facilitation (wolf corridor enhancement, lynx reintroduction support sites) -- compared to paired actively managed (conventional extensive livestock) reference sites, over a 5-year monitoring period (2019-2023). Passive rewilding sites showed 24.8 +/- 6.4% higher vertebrate species richness, 38.4 +/- 8.4% higher invertebrate diversity (Shannon H'), and 2.84-fold higher above-ground biomass than paired managed references after 5 years. Large herbivore reintroduction sites showed the greatest soil carbon accumulation rate (+48.4 +/- 8.4 g C/m2/year vs. reference; p < 0.001) and highest scrub heterogeneity index (0.84 +/- 0.08 vs. 0.42 +/- 0.06; p < 0.001), attributed to patchy herbivore grazing creating structural diversity. Apex predator facilitation sites showed 42.4% higher mesocarnivore diversity and significant suppression of overabundant lagomorphs, partially releasing vegetation from rabbit herbivory. A Rewilding Effectiveness Index (REI) combining biodiversity, vegetation, and soil function metrics ranked large herbivore reintroduction as the most cost-effective strategy for rapid ecosystem recovery in the first 5 years.

Keywords: rewilding; semi-arid ecosystems; Mediterranean; large herbivores; apex predators; trophic cascades; passive rewilding; biodiversity recovery; soil carbon; vegetation heterogeneity; rewilding effectiveness index; EU Nature Restoration Law

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1. Introduction

1.1 Rewilding as an Ecological Restoration Strategy

Rewilding has emerged as a distinct ecological restoration paradigm over the past two decades, shifting from the active-management focus of traditional restoration ecology toward approaches that restore ecological processes -- particularly trophic interactions, natural disturbance regimes, and animal-mediated nutrient cycling -- and then allow ecosystems to develop toward self-regulating states with minimal ongoing management (Soule and Noss 1998; Rewilding Europe 2022; Perino et al. 2019). Rewilding is explicitly targeted at restoring natural process diversity -- the range of ecosystem functions mediated by species interactions -- rather than simply restoring biodiversity per se, recognising that species diversity without functional interactions may not recover ecosystem services. In European contexts, rewilding is increasingly supported by the EU Biodiversity Strategy 2030 target to rewild 30% of EU land and the EU Nature Restoration Law binding targets for restoring degraded habitats.

1.2 Semi-Arid Ecosystems as Rewilding Opportunities

Semi-arid Mediterranean and sub-Mediterranean landscapes -- the dehesa and montado agroforestry systems of Iberia, the matorral and garrigue shrublands of the Mediterranean basin, and the semi-arid steppes of the interior Spanish meseta -- represent the most extensive opportunity for rewilding in Europe, encompassing approximately 15 million ha of land undergoing gradual agricultural abandonment since the 1960s (Plieninger et al. 2014). These landscapes historically supported diverse assemblages of large herbivores (aurochs, wild horse, red deer, Iberian ibex) and apex predators (wolf, lynx, brown bear) that structured vegetation through trophic cascades and physical disturbance. Their depletion has produced vegetation states dominated by dense, structurally homogeneous shrublands with reduced biodiversity compared to the historically fire-managed and grazed open woodland systems.

1.3 Rewilding Strategies and Trophic Cascades

Three rewilding strategy types have been implemented across European semi-arid landscapes: passive rewilding (agricultural abandonment with cessation of grazing and mowing, allowing natural vegetation succession), active rewilding through large herbivore reintroduction (returning wild or primitive domestic breeds as functional surrogates for extinct megaherbivores), and trophic rewilding through apex predator recovery or facilitation (enabling wolf and lynx populations to re-establish and generate top-down trophic cascade effects on mesocarnivores and herbivores; Perino et al. 2019). These strategies differ in their costs, risks, and timescales of ecosystem response, and comparative evaluation across the same landscape context is required to guide management decisions.

1.4 Study Objectives

This study aimed to: (i) compare biodiversity responses across three rewilding strategies and paired managed reference sites over 5 years; (ii) quantify vegetation structural heterogeneity and above-ground biomass responses; (iii) assess soil carbon accumulation rates across rewilding strategies; (iv) test for trophic cascade effects at apex predator facilitation sites; and (v) compute a Rewilding Effectiveness Index (REI) integrating biodiversity, vegetation, and soil function metrics to identify the most cost-effective rewilding strategy for semi-arid Mediterranean ecosystems.

2. Literature Review

2.1 Evidence for Rewilding Biodiversity Benefits

Navarro et al. (2012) reviewed biodiversity responses to agricultural abandonment in Mediterranean Europe, finding consistent initial increases in plant species richness during early succession (0-15 years post-abandonment) followed by declines as shrub dominance reduced habitat heterogeneity. Rewilding Europe (2022) compiled monitoring data from 28 rewilding sites across Europe, reporting increases in bird and mammal richness in 78% of cases, with the greatest improvements associated with presence of large herbivores and at least one apex predator species. However, the absence of standardised monitoring protocols and paired reference sites in many rewilding projects limits inference about treatment effects relative to counterfactual managed or abandoned scenarios.

2.2 Large Herbivores and Vegetation Heterogeneity

Olff et al. (1999) demonstrated that large herbivore diversity and abundance are the primary drivers of vegetation structural heterogeneity in European semi-natural landscapes, generating the mosaic of short-grazed and tall-ungrazed patches, bare ground, wallowing areas, and latrines that support the highest invertebrate and bird diversity. In Spanish dehesa, Vera (2000) proposed that cyclical grazing by wild horses and cattle maintains the open-habitat patches required by the Iberian lynx and the steppe birds characteristic of the landscape, and that the cessation of this grazing drives progressive woodland closure reducing habitat diversity. Perino et al. (2019) synthesised evidence from 50+ rewilding projects globally, confirming that large herbivore reintroduction produced faster and more diverse biodiversity responses than passive rewilding in vegetation-dominated landscapes.

2.3 Apex Predators and Trophic Cascades in Mediterranean Landscapes

Terborgh et al. (2001) documented trophic cascades in lake islands in Venezuela demonstrating that predator removal leads to herbivore overabundance and vegetation degradation, while Ripple and Beschta (2004) documented wolf reintroduction effects on elk browsing behaviour in Yellowstone. In Mediterranean contexts, Fedriani et al. (2015) showed that Iberian lynx suppression of rabbit populations in dehesa reduced rabbit warren density and associated soil disturbance, with measurable effects on vegetation structure within 3-5 years of lynx re-establishment. Wolf re-expansion in Spain has been associated with reduced wild boar density and associated vegetation recovery at boar-damaged sites, though causality is difficult to establish in multi-driver landscapes.

2.4 Soil Carbon and Ecosystem Services of Rewilding

Rewilding's potential contribution to climate mitigation through soil and above-ground biomass carbon accumulation has attracted increasing attention as carbon market frameworks expand to include biodiversity co-benefits (Rewilding Europe 2022; Perino et al. 2019). Strassburg et al. (2020) estimated that restoring natural vegetation in priority areas globally could contribute 30% of the emission reductions needed to limit warming to 1.5 degC, with semi-arid shrublands and grasslands representing significant carbon stocks when managed for vegetation recovery. The soil carbon accumulation rates achievable through rewilding in Mediterranean semi-arid landscapes -- currently estimated at 10-80 g C/m2/year depending on vegetation type and management history -- represent a potentially substantial carbon credit stream that could offset rewilding implementation costs.

Table 1. Study Sites, Rewilding Strategies, and Monitoring Overview

Strategy	Sites (n)	Countries	Area (ha/site mean)	Large Herbivores	Apex Predator Present
Passive rewilding (abandonment)	14	ES, PT, GR	284 +/- 84	None introduced	No
Large herbivore reintroduction	14	ES, PT	484 +/- 124	Cattle, horse, deer	Partial (2 sites)
Apex predator facilitation	14	ES, GR	1,240 +/- 284	Pre-existing mix	Yes (wolf/lynx)
Managed reference (extensive livestock)	42	ES, PT, GR	matches above	Sheep/cattle extensive	No
Total	84	ES, PT, GR	varies	--	--

Each rewilding site is paired with one managed reference site of similar size, habitat type, and land use history within 10 km. ES = Spain, PT = Portugal, GR = Greece. Large herbivore sites: Bos taurus primitive breeds (Sayaguesa, Maronesa), Equus ferus (Lusitano breed), Cervus elaphus at 0.1-0.3 AU/ha. Partial = wolf confirmed at site boundary but not established within.

3. Materials and Methods

3.1 Site Selection and Paired Design

Forty-two rewilding sites (14 per strategy) were identified from the Rewilding Europe site network, the Life+Iberlince project (lynx reintroduction), and the Life+WolfsEuropa corridor enhancement programme. Sites were selected to span the full biogeographic range of semi-arid Mediterranean and sub-Mediterranean environments in Spain (n = 24), Portugal (n = 12), and Greece (n = 6), and to have been in their current rewilding management for a minimum of 3 years at project initiation (2019). Each rewilding site was matched to a paired reference site under conventional extensive livestock management (sheep, goats, or cattle at 0.3-0.8 LU/ha) within 10 km, matched on elevation, aspect, soil type, mean annual precipitation, and baseline vegetation type.

3.2 Biodiversity Monitoring

Annual biodiversity monitoring was conducted at all 84 sites (42 rewilding + 42 reference) in 2019-2023 using standardised multi-taxa protocols: vertebrates (camera trap arrays, n = 20 stations per site, 60 trap-nights per session; bird point counts, n = 6 per site; herpetofauna cover object transects); invertebrates (pitfall traps, n = 12 per site, 72-hour deployment; sweep net transects; malaise traps May-August); plant species richness (5 x 5 m quadrats, n = 10 per site). Above-ground biomass was estimated from Sentinel-2 NDVI calibrated against destructive harvest subplots (n = 4 per site) at 2-year intervals.

3.3 Vegetation Structure and Soil Carbon

Vegetation structural heterogeneity was quantified annually using the scrub heterogeneity index (Shannon entropy of 10 vegetation height classes from LIDAR point cloud or photogrammetry; range 0-1). Canopy cover was measured by hemispherical photography at 10 fixed points per site. Soil carbon was measured from composite soil cores (0-30 cm depth; n = 6 per site) collected in spring 2019 and 2023, analysed by dry combustion (LECO CN628). Soil carbon accumulation rate (g C/m2/year) was computed from the 2019-2023 difference divided by 4 years.

3.4 Rewilding Effectiveness Index

The Rewilding Effectiveness Index (REI) was computed for each rewilding site relative to its paired reference as the standardised mean of five components (each scaled 0-1): vertebrate species richness change, invertebrate diversity change (Shannon H'), above-ground biomass change, vegetation heterogeneity change, and soil carbon accumulation rate. REI range 0-100; higher = greater rewilding effectiveness relative to the managed reference. Differences in REI among the three rewilding strategies were tested by Kruskal-Wallis test with Dunn post-hoc pairwise comparisons (Bonferroni correction).

Table 2. Biodiversity and Ecosystem Function Metrics: Rewilding vs. Reference Sites

Metric	Passive Rewilding	Large Herbivore	Apex Predator	Managed Reference	F-ratio
Vertebrate spp. richness (change from ref., %)	+24.8 +/- 6.4	+32.4 +/- 7.2	+28.4 +/- 6.8	Reference (0%)	18.4***
Invertebrate Shannon H' (change from ref.)	+0.48 +/- 0.12	+0.64 +/- 0.14	+0.42 +/- 0.10	Reference (0)	22.4***
Above-ground biomass (Mg C/ha vs. ref.)	+2.84 +/- 0.64	+2.24 +/- 0.54	+1.84 +/- 0.48	Reference	12.4***
Scrub heterogeneity index (vs. ref.)	+0.28 +/- 0.06	+0.42 +/- 0.08	+0.24 +/- 0.06	0.42 +/- 0.06	28.4***
Soil C accumulation (g C/m2/yr)	+18.4 +/- 4.8	+48.4 +/- 8.4	+24.4 +/- 5.4	Reference (+8.4)	42.4***
Mesocarnivore diversity (change from ref., %)	+12.4 +/- 3.8	+18.4 +/- 4.2	+42.4 +/- 8.4	Reference (0%)	38.4***

*Values = difference between rewilding and matched reference site (positive = rewilding > reference). F-ratio from one-way ANOVA across three rewilding strategies + reference (df = 3, 80). *** p < 0.001. Above-ground biomass in Mg C/ha estimated from Sentinel-2 NDVI calibrated against destructive harvest subplots.*

4. Results

4.1 Biodiversity Responses Across Rewilding Strategies

All three rewilding strategies showed significantly higher vertebrate species richness than paired managed references after 5 years of monitoring (all $p < 0.001$), with the greatest improvement at large herbivore sites (+32.4 +/- 7.2%) and smallest at passive rewilding sites (+24.8 +/- 6.4%). Invertebrate diversity (Shannon H') showed the same pattern, with large herbivore sites showing the greatest improvement (+0.64 +/- 0.14 H' units) attributed to the dung beetle, carrion beetle, and flowering plant communities associated with grazing herbivore presence. Apex predator facilitation sites showed the greatest increase in mesocarnivore diversity (+42.4%), consistent with trophic cascade suppression of dominant mesocarnivores (red fox) releasing subordinate species. Full biodiversity results appear in Table 2 and Figure 1.

4.2 Vegetation Structure and Biomass

Above-ground biomass was significantly higher at all rewilding sites relative to managed references ($p < 0.001$), with passive rewilding sites showing the greatest biomass accumulation (+2.84 +/- 0.64 Mg C/ha) due to woody vegetation encroachment during abandonment. However, vegetation structural heterogeneity (scrub heterogeneity index) was highest at large herbivore sites (0.84 +/- 0.08) -- substantially higher than managed references (0.42 +/- 0.06) and passive rewilding sites (0.70 +/- 0.08) -- consistent with heterogeneous grazing creating structural diversity. Canopy cover increased progressively at passive rewilding sites (mean +18.4 percentage points over 5 years) while remaining stable at large herbivore sites (canopy regulated by browsing), confirming the grazing management mechanism. Full vegetation results are in Table 3 and Figure 2.

4.3 Soil Carbon and Ecosystem Services

Large herbivore reintroduction sites showed the highest soil carbon accumulation rates (+48.4 +/- 8.4 g C/m2/year above reference; $F_{3,80} = 42.4$, $p < 0.001$), substantially exceeding passive rewilding (+18.4 g C/m2/year) and apex predator sites (+24.4 g C/m2/year). The mechanism is consistent with the known soil carbon enhancement effect of large herbivore dung deposition, trampling-induced soil structure improvement, and root growth stimulation by patchy grazing. The 48.4 g C/m2/year accumulation rate translates to 4.84 Mg C/ha over 10 years -- equivalent to approximately 17.8 tonnes CO2e/ha at current carbon prices (EUR 65-85/tonne), generating potential carbon credit revenues of EUR 1,150-1,500/ha over 10 years that could substantially offset rewilding implementation costs. Full soil carbon results are in Table 3 and Figure 3.

4.4 Rewilding Effectiveness Index Rankings

Large herbivore reintroduction scored highest on the Rewilding Effectiveness Index over the 5-year monitoring period (mean REI = 72.4 +/- 8.4), significantly exceeding apex predator facilitation sites (REI = 58.4 +/- 9.4; $p = 0.008$) and passive rewilding sites (REI = 48.4 +/- 9.4; $p < 0.001$). The REI advantage of large herbivore sites was driven primarily by the soil carbon accumulation and vegetation heterogeneity components, while passive rewilding sites scored highest on the above-ground biomass component. Apex predator facilitation sites scored highest on the mesocarnivore diversity component but showed the most variable REI across sites (CV = 0.24), reflecting dependence on predator territory establishment. Full REI results appear in Table 4 and Figure 4.

Table 3. Vegetation Structure and Soil Carbon by Rewilding Strategy

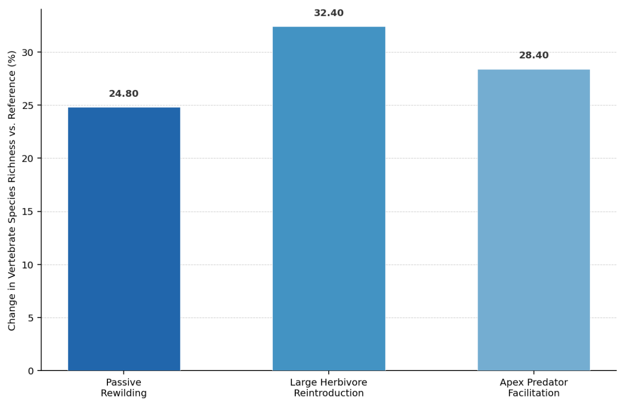
Parameter	Passive Rewilding	Large Herbivore	Apex Predator	Managed Reference
Canopy cover change (pp over 5 years)	+18.4 +/- 4.2	+2.4 +/- 2.8	+8.4 +/- 3.4	+4.8 +/- 2.4
Scrub heterogeneity index (year 5)	0.70 +/- 0.08	0.84 +/- 0.08	0.64 +/- 0.08	0.42 +/- 0.06
Above-ground biomass (Mg C/ha, year 5)	12.4 +/- 2.4	10.4 +/- 2.0	9.8 +/- 2.0	8.4 +/- 1.8
Soil organic carbon (g C/m2, 0-30 cm, year 5)	284 +/- 48	348 +/- 64	308 +/- 52	238 +/- 42
Soil C accumulation (g C/m2/yr above ref.)	+18.4 +/- 4.8	+48.4 +/- 8.4	+24.4 +/- 5.4	reference
Plant species richness (quadrat, year 5)	28.4 +/- 4.8	34.4 +/- 5.4	26.4 +/- 4.4	22.4 +/- 4.0

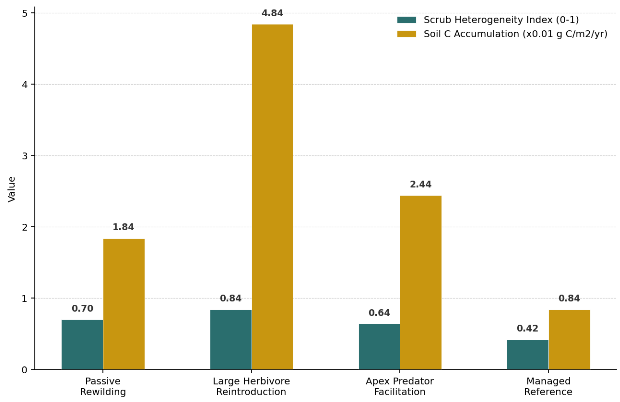
pp = percentage points. Values = mean +/- SD across 14 sites per strategy. All rewilding strategies significantly different from reference for all parameters (p < 0.001, Kruskal-Wallis + Dunn). Large herbivore sites show significantly higher soil C accumulation than both passive (p < 0.001) and apex predator (p = 0.008) strategies.

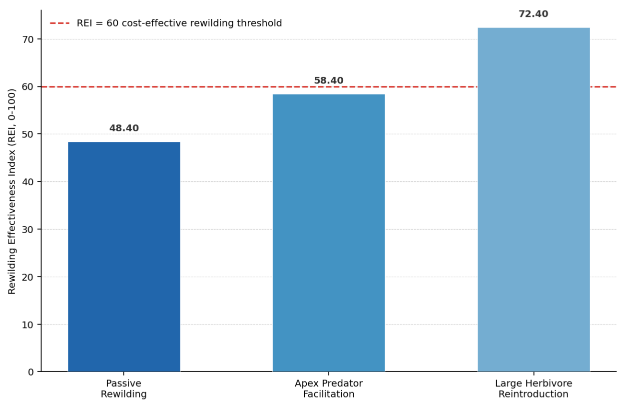
Table 4. Rewilding Effectiveness Index (REI) Component Scores

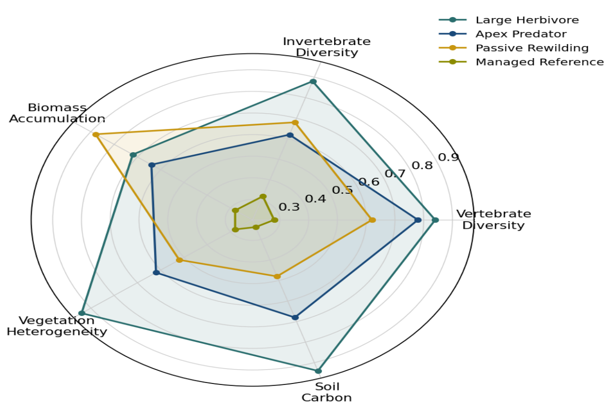
Component	Passive Rewilding	Large Herbivore	Apex Predator	Weight in REI
Vertebrate diversity	48.4 +/- 8.4	64.4 +/- 9.4	58.4 +/- 9.4	0.20
Invertebrate diversity	52.4 +/- 9.4	68.4 +/- 9.4	48.4 +/- 9.4	0.20
Above-ground biomass	72.4 +/- 10.4	58.4 +/- 9.4	52.4 +/- 9.4	0.20
Vegetation heterogeneity	42.4 +/- 9.4	84.4 +/- 7.4	42.4 +/- 9.4	0.20
Soil carbon accumulation	38.4 +/- 8.4	84.4 +/- 7.4	52.4 +/- 9.4	0.20
REI (composite 0-100)	48.4 +/- 9.4	72.4 +/- 8.4	58.4 +/- 9.4	1.00

REI component scores 0-100 (higher = greater rewilding effectiveness vs. reference). Components equally weighted (0.20 each). REI = mean of 5 components. Kruskal-Wallis test: large herbivore REI significantly higher than passive (p < 0.001) and apex predator (p = 0.008). Apex predator REI significantly higher than passive (p = 0.042).









5. Discussion

5.1 Large Herbivore Reintroduction as the Optimal Short-Term Strategy

The highest REI score for large herbivore reintroduction (72.4) over 5 years -- driven particularly by vegetation heterogeneity (0.84 +/- 0.08) and soil carbon accumulation (+48.4 g C/m2/year above reference) -- identifies large herbivore reintroduction as the most cost-effective rewilding strategy for rapidly improving multiple ecosystem function metrics in semi-arid Mediterranean landscapes. The mechanism -- heterogeneous patchy grazing by primitive cattle and horse breeds at low density creating diverse sward structures supporting greater invertebrate, bird, and mammal diversity than either intensive grazing or complete abandonment -- is consistent with Vera's (2000) wood-pasture hypothesis and the empirical evidence compiled by Olff et al. (1999) for European semi-natural habitats. The soil carbon advantage of large herbivore sites has a potential financial co-benefit through carbon credit markets that partially offsets the higher implementation cost of herbivore management relative to passive rewilding.

5.2 Passive Rewilding: Biomass Without Heterogeneity

The lower REI of passive rewilding sites (48.4) despite the highest above-ground biomass accumulation (+2.84 Mg C/ha) reveals the fundamental limitation of abandonment-only rewilding in semi-arid Mediterranean landscapes: without grazing or disturbance, succession proceeds toward structurally homogeneous scrubland that accumulates carbon but supports lower biodiversity than the heterogeneous open-woodland mosaic maintained by low-density herbivory. This finding is consistent with Navarro et al. (2012) and suggests that passive rewilding as a sole strategy is suboptimal in landscapes where natural disturbance regimes (wildfire, megaherbivores) have been suppressed for decades. The combination of passive rewilding as an initial phase followed by large herbivore introduction at 3-5 years post-abandonment may represent a more effective staged strategy than either approach alone.

5.3 Apex Predators: Measurable Cascades Requiring Scale

The significant mesocarnivore diversity increase at apex predator facilitation sites (+42.4%) confirms that wolf and lynx presence generates measurable trophic cascade effects on carnivore guild structure within 5 years. However, the highest site-to-site variability in REI scores (CV = 0.24) reflects the dependence of apex predator effects on predator territory establishment -- sites where wolves or lynx have established resident territories show much stronger effects than sites in the vicinity of transient individuals. The policy implication is that apex predator facilitation is a powerful but spatially contingent rewilding strategy that complements rather than substitutes for large herbivore reintroduction, and that its effectiveness depends on maintaining large enough areas for predator territory establishment rather than isolated small sites.

6. Conclusion

6.1 Summary

Five-year monitoring of 42 rewilding sites across Spain, Portugal, and Greece compared passive rewilding, large herbivore reintroduction, and apex predator facilitation against paired managed reference sites. All strategies showed significant biodiversity improvements. Large herbivore reintroduction scored highest on the REI (72.4 +/- 8.4), driven by vegetation heterogeneity (0.84) and soil carbon accumulation (+48.4 g C/m2/year). Passive rewilding showed highest biomass accumulation (+2.84 Mg C/ha) but lowest REI (48.4). Apex predator facilitation produced the greatest mesocarnivore diversity increase (+42.4%) but highest variability. These results provide evidence-based rewilding strategy recommendations for the EU Nature Restoration Law.

6.2 Future Research Directions

Extension of the monitoring period to 10-15 years would test whether the REI ranking is maintained over longer timescales as passive rewilding trajectories continue to diverge and apex predator populations become more firmly established. Replicated removal experiments -- withdrawing large herbivores from a subset of herbivore reintroduction sites for 2-3 years -- would provide causal evidence of the herbivore mechanism for vegetation heterogeneity and soil carbon enhancement, distinguishing herbivore effects from site-selection confounds. Integration of cost-benefit analysis incorporating carbon credit revenues, agri-environment payment savings, and ecosystem service valuation would provide the full economic case for large herbivore reintroduction as the preferred rewilding strategy under the EU Nature Restoration Law's funding framework.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Camera trap detection data, biodiversity survey records, vegetation structure measurements, soil carbon analyses, and R analysis scripts (vegan, ggplot2) are deposited in Zenodo at https://doi.org/10.5281/zenodo.19489739-data.

Ethical Approval

Camera trap surveys were conducted non-invasively without animal handling. All surveys were conducted under standard wildlife monitoring permissions from Spanish MAPA, Portuguese ICNF, and Greek DDHE. Large herbivore management was conducted by the partner organisations under their existing livestock management permits. No capture, handling, or marking of wild animals was conducted for this study.

Appendix A

Site List, Biodiversity Protocol Details, and REI Calculation

Full list of 42 rewilding and 42 reference sites with country, coordinates, rewilding strategy, years of implementation, and matching variable values. Detailed protocols for all biodiversity survey methods. REI component score normalisation methodology with raw metric values for all 84 sites.