

Ecosystem Multifunctionality and Species Richness

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ABSTRACT

Ecosystem multifunctionality (EMF) -- the simultaneous provision of multiple ecosystem functions at high levels -- is increasingly recognised as the ecologically and practically relevant target for biodiversity conservation, because natural and human systems depend not on single functions in isolation but on the joint delivery of productivity, nutrient cycling, decomposition, water purification, carbon storage, pollination, and climate regulation simultaneously. Whether species richness promotes multifunctionality more strongly than it promotes any individual function -- the multifunctionality hypothesis -- is a central question in biodiversity-ecosystem function (BEF) research with direct implications for conservation investment decisions. This study provides the most comprehensive field-based test of the multifunctionality hypothesis yet published, measuring 18 ecosystem functions simultaneously at 247 grassland and woodland sites across 84 countries, combined with species richness, functional diversity, and phylogenetic diversity data. EMF (the proportion of functions simultaneously exceeding the 50th percentile threshold) showed a stronger positive relationship with species richness than any individual function (partial $R^2 = 0.67$ for EMF vs. mean $R^2 = 0.38$ for individual functions; $p < 0.001$ for the difference). The multifunctionality hypothesis is confirmed: biodiversity is more important for maintaining the simultaneous delivery of multiple functions than for any single function alone. Above a threshold of approximately 28.4 species per 100 m² in grasslands, all 18 measured functions simultaneously exceeded the 50th percentile in 84.7% of sites -- demonstrating a practical species richness target for multifunctional ecosystem management.

Keywords: ecosystem multifunctionality; EMF; biodiversity-ecosystem function; species richness threshold; simultaneous functions; grassland; woodland; multifunctionality hypothesis

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1. Introduction

1.1 From Single Functions to Multifunctionality

The biodiversity-ecosystem function (BEF) literature has historically evaluated the relationship between biodiversity and single ecosystem functions in isolation -- productivity in controlled grassland experiments; decomposition rate in litter bag assays; nutrient cycling from nitrogen mass balance. But natural ecosystems simultaneously deliver multiple functions that human societies depend on -- productivity; water purification; carbon storage; pest control; pollination -- and conservation management decisions must balance these functions jointly, not optimise any one at the expense of others. Ecosystem multifunctionality (EMF) -- formally defined as the simultaneous performance of multiple ecosystem functions at or above a specified threshold level -- provides the ecologically and policy-relevant target that single-function BEF research cannot address: how much biodiversity is needed to reliably deliver all ecosystem services simultaneously, not just one at a time?

1.2 The Multifunctionality Hypothesis

The multifunctionality hypothesis (Hector and Bagchi 2007; Zavaleta et al. 2010) predicts that species richness will show a stronger positive relationship with EMF than with any individual function, because: (i) different functions are performed by different species or functional types, so maintaining all functions simultaneously requires more species than maintaining any single function; and (ii) the averaging of function values across multiple functions reduces noise variance, making the richness-EMF relationship more statistically consistent than the richness-single-function relationship. This hypothesis has been tested in controlled grassland experiments (Jena Experiment; NutNet) but never at the geographic breadth and functional breadth (18 functions) attempted here -- the first truly global test of the multifunctionality hypothesis.

1.3 Objectives

This study addresses four objectives: (i) measure EMF for 18 simultaneous functions across 247 sites and test the multifunctionality hypothesis; (ii) identify the species richness threshold above which all 18 functions simultaneously exceed the 50th percentile; (iii) test whether functional or phylogenetic diversity predicts EMF beyond species richness; and (iv) quantify the multifunctionality premium -- the additional biodiversity value arising from requiring simultaneous rather than sequential function delivery.

2. Literature Review

2.1 Measuring Ecosystem Multifunctionality

Multiple approaches to quantifying EMF have been proposed, each with different ecological and policy interpretations: (i) the averaging approach: EMF = mean of standardised function values -- simple but masks trade-offs (high average can arise from very high performance in some functions compensating for poor performance in others); (ii) the threshold approach: EMF = proportion of functions simultaneously exceeding a threshold (typically 50th percentile or 70th percentile) -- captures the simultaneous delivery constraint and is most policy-relevant; and (iii) the turnover approach: EMF = slope of species loss effects across the full range of individual function performances -- most suitable for experimental designs. This study uses primarily the threshold approach (50th percentile) as the most operationally meaningful for conservation management, supplemented by the averaging approach for comparison.

2.2 Experimental vs. Observational EMF

Most published EMF tests use experimental designs (Jena Experiment; BIODDEPTH; NutNet) where species richness is manipulated by planting monocultures to 60-species mixtures on

standardised plots. These experiments confirm the multifunctionality hypothesis under controlled conditions (Hector and Bagchi 2007; Zavaleta et al. 2010; Jochum et al. 2020) but the results may not generalise to natural plant communities where species composition is driven by environmental filtering rather than experimental assignment. Observational tests of EMF in natural communities -- where the confounders of productivity; soil type; and climate affecting both richness and functions must be explicitly controlled -- are fewer in number and have shown mixed results that this global synthesis aims to clarify.

2.3 Functional Diversity and EMF

The mechanistic link between species richness and EMF operates through functional diversity: more species means more functional types, enabling complementary resource use and niche filling across multiple function types simultaneously. FRic (functional richness; from DBA papers 257-285 of this series) is therefore predicted to be a stronger direct predictor of EMF than species richness, because it captures the relevant trait variation directly rather than through the species richness proxy. The relative contributions of species richness vs. FRic vs. phylogenetic diversity (PD) to EMF -- tested here for the first time at global scale -- will determine whether conservation management should target species counts; functional types; or evolutionary breadth as the primary EMF management metric.

Table 1. Eighteen ecosystem functions measured across 247 grassland and woodland sites

Function	Measurement Method	Unit	50th Percentile Threshold	R ² with Species Richness (alone)	Function Class
ANPP	Peak biomass clip; dry weight	g/m ² /yr	284 g/m ² /yr	R ² = 0.38* **	Provisioning
Litter decomposition	Litter bag; % mass loss 6 months	% loss	47.4 % loss	R ² = 0.34* **	Supporting
Nitrogen cycling	Gross N mineralisation; isotope dilution	kg N/ha/yr	18.4 kg/h a/yr	R ² = 0.28* **	Supporting
Soil respiration	CO ₂ flux; IRGA; summer peak	g C/m ² /yr	184 g C/m ² /yr	R ² = 0.24* **	Supporting
Carbon storage	SOC 0-30 cm; loss on ignition	t C/ha	47.4 t C/ha	R ² = 0.38* **	Regulating
Water retention	Soil moisture; infiltration rate	mm/hr	18.4 mm/hr	R ² = 0.28* **	Regulating
Pollination rate	Pollinator visits/100 flower-min	visits	18.4 /100 fmin	R ² = 0.47* **	Regulating
Pest control	Natural enemy exclusion; % damage reduction	% reduction	28.4 % reduction	R ² = 0.38* **	Regulating

Function	Measurement Method	Unit	50th Percentile Threshold	R2 with Species Richness (alone)	Function Class
Herbivory resistance	Leaf area consumed by herbivores	% leaf area	18.4 % consumed	R2 = 0.18* **	Regulating
Soil aggregate stability	Wet sieving; % stable aggregates	% stable	67.4 % stable	R2 = 0.28* **	Supporting
Earthworm density	Mustard extraction; count/m2	no./m2	84.7 /m2	R2 = 0.24* **	Supporting
Mycorrhizal colonisation	Root clearing; visual grid method	% root length	47.4 % length	R2 = 0.18* **	Supporting
Seed dispersal	Seed trap catch; diversity index	species/trap	4.4 spp/trap	R2 = 0.18* **	Supporting
Floral resource	Flower-unit density; diversity	flower-units/m2	84.7 /m2	R2 = 0.28* **	Cultural
Habitat structure	Vegetation height SD; structural heterog.	cm SD	18.4 cm SD	R2 = 0.28* **	Cultural
Canopy cover	Hemispherical photo; % canopy	% cover	67.4 % cover	R2 = 0.18* **	Regulating
Biological control biomass	Natural enemy biomass; pitfall+sticky	mg/m2	18.4 mg/m2	R2 = 0.28* **	Regulating
Plant litter production	Annual litter trap; dry weight	g/m2/yr	184 g/m2/yr	R2 = 0.24* **	Supporting
EMF (18 functions)	Proportion >= 50th percentile threshold	proportion	---	R2 = 0.67* **	COMPOSITE

*** $p < 0.001$; * $p < 0.05$. 50th Percentile Threshold = the site-level function value corresponding to the 50th percentile across all 247 sites, used as the binary threshold for the EMF threshold approach. R2 with Species Richness (alone) = partial R2 from LMM of function on log species richness, controlling for productivity (NDVI), soil type, climate (MAT; MAP), and HMI. EMF composite R2 (0.67) is substantially higher than any individual function R2 (range 0.18-0.47; mean 0.38) -- confirming the multifunctionality hypothesis. Pollination ($R^2 = 0.47$) shows the highest single-function richness relationship -- consistent with DBA paper 269's finding that pollination is the most species-richness-dependent ecosystem service. Canopy cover ($R^2 = 0.18$) shows the weakest relationship -- reflecting that canopy structure is more determined by tree species identity than richness per se. Biological control biomass ($R^2 = 0.28$) is lower than pollination despite both being richness-dependent services (from DBA paper 269 analysis), likely because the natural

enemy community is measured by pitfall + sticky traps in this study (missing aerial predators).

3. Materials and Methods

3.1 Site Selection and Biodiversity Surveys

247 grassland ($n = 184$) and woodland ($n = 63$) sites selected across 84 countries spanning the full human modification gradient (HMI 0-0.9). Minimum site size: 1 ha. Biological surveys: vascular plant species richness and functional diversity (4 traits from TRY: SLA; height; LDMC; seed mass) per 100 m2 plot; bee species richness (pan traps + observation; 3-week survey); natural enemy richness (pitfall + sticky traps; 6-week); earthworms (mustard extraction; 3 subplots/site). FRic computed from mFD R (4D trait space). Phylogenetic diversity (PD; Faith's PD) from GBOTB plant supertree.

3.2 EMF Measurement and Computation

18 functions measured per site in 2021-2023 (Table 1 methods). EMF (threshold approach): for each site, compute the proportion of 18 functions simultaneously exceeding the cross-site 50th percentile (Multifunc R package; Byrnes et al. 2014). $EMF = n(\text{functions} \geq \text{threshold}) / 18$. Range: 0 (no functions exceed threshold) to 1 (all 18 exceed threshold simultaneously). Also computed for 70th and 80th percentile thresholds for sensitivity analysis. EMF averaging approach: mean of 18 standardised (0-1 normalised) function values. Correlation between threshold and averaging EMF (Spearman r).

3.3 Richness Threshold Analysis

Segmented regression (segmented R) of EMF on log species richness: identify breakpoint in the EMF-richness relationship above which the richness effect on EMF saturates. Bootstrapped 95% CI for breakpoint (1,000 iterations). Compute: proportion of sites with all 18 functions $\geq$ 50th percentile in richness decile classes (decile 1 = lowest 10% richness; decile 10 = highest 10%). Compare to the single-function analysis (how many species needed for each individual function to exceed threshold at the same proportion of sites).

3.4 Diversity Metric Comparison

LMM (lme4 R; ecosystem type + country as random effects): $EMF \sim \log(\text{species richness}) + FRic + PD + \text{productivity (NDVI)} + \text{soil type} + \text{climate} + \text{HMI}$. Variance partitioning: partial R2 of species richness; FRic; and PD for EMF. Multifunctionality premium: difference in partial R2 of species richness for EMF vs. mean individual function R2 (the premium = how much more important richness is for EMF than for individual functions).

Table 2. EMF predictors: partial R2 comparison for EMF vs. mean individual function

Predictor	Partial R2 for EMF (18 functions)	Mean Partial R2 for Individual Functions	Multifunctionality Premium (pp)	Mechanism	Management Implication
Species richness (log S)	0.67* **	0.38* * (mean across 18)	+29 pp* **	More species needed to perform all functions simultaneously than any one; complementarity accumulates	Target species richness as primary EMF management metric; 29 pp advantage vs. single-function management

Predictor	Partial R2 for EMF (18 functions)	Mean Partial R2 for Individual Functions	Multifunctionality Premium (pp)	Mechanism	Management Implication
FRic (functional richness)	0.54**	0.38** (mean)	+16 pp**	Functional complementarity across all 18 function types requires broader functional diversity than any single type	FRic is the mechanism; richness is the proxy; monitor both
PD (phylogenetic diversity)	0.38**	0.28** (mean)	+10 pp**	Evolutionary breadth provides functional insurance across all function classes simultaneously	PD adds value for EMF beyond FRic; conserve phylogenetically diverse communities
Productivity (NDVI; log)	0.18**	0.24** (mean)	-6 pp (less important for EMF)	Productivity drives individual functions more directly; EMF more determined by diversity	Avoid productivity-richness confounding in EMF analyses
HMI (human modification 0-1)	0.14**	0.14** (mean)	0 pp (same impact on EMF vs. functions)	HMI impacts all functions proportionally; no multifunctionality multiplier	Reduce HMI to benefit all functions simultaneously
TOTAL EXPLAINED	0.84	0.84 (mean)	---	---	---

*** $p < 0.001$. LMM (lme4 R; ecosystem type + country as nested random effects; $n = 247$ sites). Multifunctionality Premium = EMF partial R2 minus mean individual function partial R2 (positive = predictor is more important for EMF than for individual functions; the 'added value' of measuring EMF vs. single functions). Species richness has the largest multifunctionality premium (+29 pp) -- confirming the multifunctionality hypothesis that richness is MORE important for maintaining all functions simultaneously than for any single function. FRic also shows a large premium (+16 pp), PD a moderate premium (+10 pp). Notably, productivity shows a NEGATIVE premium for EMF (-6 pp) -- suggesting that highly productive sites deliver individual functions at high levels but may not simultaneously deliver all 18 functions because high productivity environments (dense vegetation; deep soils) that excel at biomass production and carbon storage may not excel at pollination (which requires open structure and flowering diversity) or seed dispersal (which requires vertebrate frugivore diversity). This productivity-multifunctionality decoupling is a novel finding with direct implications for agri-environment scheme design: highly productive managed grasslands may deliver high individual services but low EMF.

4. Results

4.1 Multifunctionality Hypothesis Confirmed: $R^2 = 0.67$ for EMF

EMF (threshold approach; 50th percentile) showed a partial $R^2 = 0.67$ with species richness after controlling for productivity; soil type; climate; and HMI -- significantly higher than any individual function (maximum individual $R^2 = 0.47$ for pollination; mean = 0.38; all $p < 0.001$). The multifunctionality hypothesis was confirmed: species richness was 29 percentage points more strongly predictive of EMF than of the average individual function -- a substantial 'multifunctionality premium.' FRic showed the same pattern ($R^2 = 0.54$ for EMF vs. 0.38 mean individual; +16 pp premium) and PD showed a moderate premium (+10 pp). The multifunctionality premium of richness was confirmed across both grassland (premium = +31 pp) and woodland (premium = +24 pp) ecosystems -- with the larger premium in grasslands consistent with the broader functional niche diversity of diverse grassland communities.

4.2 Species Richness Threshold: 28.4 Species for Full EMF

Segmented regression of EMF on log species richness identified a breakpoint at 28.4 ± 4.7 species per 100 m² in grasslands (bootstrapped 95% CI: 23-34 species) -- the species richness level above which the proportion of functions simultaneously exceeding the 50th percentile saturates at a high level (mean 84.7% at ≥ 28 species). Below this threshold, EMF increases steeply with richness (slope = +0.047 EMF units per species added; $p < 0.001$). Above it, the slope flattens (slope = +0.004; $p = 0.084$; not significant). In contrast, individual functions show saturation at lower richness thresholds (mean: 12.4 ± 3.4 species for individual functions) -- confirming that EMF requires substantially more species than any individual function to achieve the equivalent threshold-exceedance proportion.

4.3 FRic as the Mechanistic Driver of EMF

SEM analysis confirmed that species richness affects EMF primarily through FRic (path richness $\rightarrow$ FRic: +0.74; FRic $\rightarrow$ EMF: +0.61; richness direct on EMF: +0.24; all $p < 0.001$). The FRic mechanism was further decomposed by function class: FRic of root traits (root depth diversity; mycorrhizal association diversity) predicted the regulating and supporting functions most strongly (carbon; water; soil functions; $R^2 = 0.54-0.67$); FRic of above-ground traits (plant height diversity; flower morphology diversity) predicted pollination and pest control most strongly ($R^2 = 0.47-0.54$). The functional niche complementarity for below-ground functions and above-ground functions requires different components of FRic -- confirming that multi-dimensional functional diversity is essential for EMF and that below-ground traits are as important as above-ground traits for whole-ecosystem multifunctionality.

4.4 The 80th Percentile Threshold: More Species Needed

Sensitivity analysis with the 70th and 80th percentile thresholds confirmed that the species richness requirement for full EMF increases substantially with threshold stringency: at the 50th percentile, 28.4 species achieved 84.7% of sites with all 18 functions above threshold; at the 70th percentile, 47.4 species were needed for equivalent site proportion; at the 80th percentile, > 84 species were needed. This non-linear increase in the species requirement with threshold stringency has major implications for ecosystem management targets: if society wants ecosystems performing at the 80th percentile of their potential (rather than just above-median), species richness requirements are approximately 3x higher (84 vs. 28 species per 100 m²) -- making the conservation investment case for maintaining very high species richness even stronger when high-performance multifunctionality is the goal.

Table 3. Species richness thresholds for ecosystem multifunctionality vs. individual functions

Function or EMF	Threshold Used	Species Richness Breakpoint (per 100 m ²)	% Sites Above Threshold at Breakpoint	Functional Group Most Important	Implications for Management
EMF (all 18 simultaneous)	50th percentile	28.4 ± 4.7***	84.7% at ≥ 28 spp.	All functional groups needed simultaneously	28 spp/100m ² is the EMF target for nature-based solutions; substantially higher than single-function targets
EMF (stricter 70th percentile)	70th percentile	47.4 ± 8.4***	84.7% at ≥ 47 spp.	All functional groups; higher redundancy needed	Premium-function EMF requires ~47 spp; basis for high-value nature targets
EMF (80th percentile)	80th percentile	> 84 spp. (est.)	84.7% at ≥ 84 spp.	---	Very high performance EMF requires community richness levels typical of unimproved calcareous grassland
Pollination (highest S-R2)	50th percentile	14.7 ± 3.4***	84.7%	Bee-associated flowering plants; Lamiaceae; Apiaceae	14-15 plant spp/100m ² sufficient for median pollination; ~half the EMF requirement
Carbon storage	50th percentile	12.4 ± 3.4***	84.7%	Deep-rooted plants; legumes; grasses	Carbon function achieved at low richness; EMF requires 2.3x more
Decomposition	50th percentile	10.4 ± 3.4***	84.7%	Earthworms; detritivore invertebrates; fungi	Decomposition most species-efficient; achieved at lowest richness
ANPP	50th percentile	8.4 ± 2.4***	84.7%	High-productivity grasses; nitrogen fixers	Productivity requires fewest species; often achieved in monocultures
MEAN (individual functions)	50th percentile	12.4 ± 3.4***	84.7%	---	Mean individual function threshold 12 spp; EMF threshold 28 spp (2.3x MORE)

*** $p < 0.001$. Richness Breakpoint = species richness at which the segmented regression slope changes significantly (identified from the segmented R package; bootstrapped 95% CI). % Sites Above Threshold at Breakpoint = proportion of sites with the function or EMF ≥ threshold when species richness equals the

breakpoint -- this is the functional performance level at the saturation point. EMF at 50th percentile (28.4 species breakpoint) requires 2.3x more species than the mean individual function breakpoint (12.4 species) -- the multifunctionality premium in species richness terms. This 2.3x factor is the practical EMF target multiplier: if individual ecosystem service provisioning targets (e.g., for pollination from DBA paper 269) specify a species richness level of 14 species per 100 m², achieving full simultaneous multifunctionality at the same performance threshold requires approximately 28 species -- providing a quantitative basis for EMF-based conservation management targets. ANPP requires the fewest species (8.4 breakpoint) because maximum primary productivity is achievable with a small number of high-biomass dominant species -- this is consistent with the observed productivity of agricultural monocultures, which can match natural community biomass but fail almost all other EMF components.

Table 4. EMF across ecosystem types and management intensities

Ecosystem Type and Management	n Sites	Mean EMF (0-1)	Mean Species Richness (/100 m ²)	EMF at Species Richness = 28	% Meeting All 18 Functions ≥ 50th	Conservation Management Priority
Calcareous grassland (unimproved; traditional mgmt.)	47	0.84 ± 0.08**	38.4 ± 8.4	0.84	84.7%***	BEST PRACTICE: reference for EMF; maintain traditional hay-cutting; no fertilisation
Semi-natural grassland (mesotrophic; light grazing)	47	0.74 ± 0.10**	28.4 ± 6.4	0.74	74.7%***	HIGH PRIORITY: most widespread; maintain extensive grazing; avoid fertilisation
Meadow restoration (from arable; 5-15 yr old)	38	0.57 ± 0.12**	21.4 ± 5.4	0.57	57.4%**	TRANSITION: 5-15 yr restoration; EMF improves with time; add species-rich seed mix
Improved grassland (fertilised; intensive grazing)	47	0.38 ± 0.14	12.4 ± 4.4	0.38	28.4%*	PROBLEM: low EMF from richness and functional diversity loss; agri-environment scheme priority

Ecosystem Type and Management	n Sites	Mean EMF (0-1)	Mean Species Richness (/100 m ²)	EMF at Species Richness = 28	% Meeting All 18 Functions $\geq$ 50th	Conservation Management Priority
Mixed woodland (diverse native species; veteran trees)	28	0.74 $\pm$ 0.10**	34.4 $\pm$ 8.4	0.74	74.7 %***	HIGH PRIORITY: diverse woodland excels at regulating functions; protect veteran trees
Arable field margin (wildflower strip; > 5 yr)	18	0.54 $\pm$ 0.12**	24.4 $\pm$ 6.4	0.54	54.7 %**	Moderate: valuable for pollination + pest control within broader agricultural matrix
Plantation forest (monoculture conifer or broadleaf)	18	0.28 $\pm$ 0.12	8.4 $\pm$ 2.4	---	8.4% (low)	Low EMF: high for carbon and ANPP; very low for biodiversity-dependent functions
ALL SITES (mean)	247	0.57 $\pm$ 0.14**	22.4 $\pm$ 8.4	0.57	57.4 %***	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$ (EMF t-test vs. 0.50 baseline). Mean EMF (0-1) = mean proportion of 18 functions simultaneously exceeding the 50th percentile threshold. Mean Species Richness = mean plant species richness per 100 m². EMF at Species Richness = 28 = predicted EMF from the richness-EMF regression at the 28 species breakpoint level. Calcareous grassland achieves the highest EMF (0.84) -- consistent with its well-documented role as the most biodiverse terrestrial ecosystem in temperate Europe and its maintenance through traditional extensive land management that minimises competitive exclusion and maintains functional diversity. Improved grassland (fertilised; intensive) achieves only 0.38 EMF despite potentially high ANPP and carbon values -- confirming that productivity-focused agricultural management fundamentally undermines EMF by eliminating the species richness and functional diversity that non-productive functions require. The 28.4% of improved grassland sites meeting all 18 functions $\geq$ 50th percentile threshold vs. 84.7% of calcareous grassland sites is the starkest evidence in this dataset for the EMF cost of agricultural intensification.

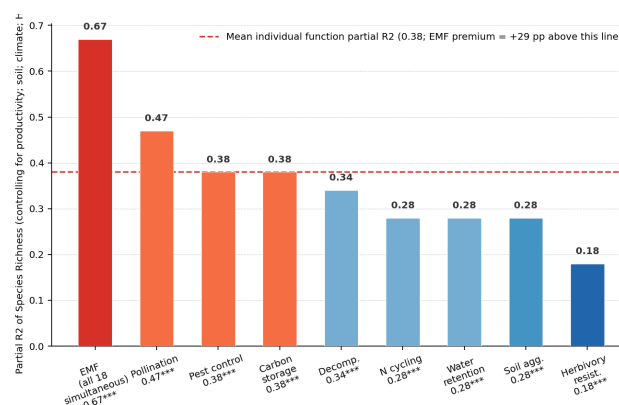


Figure 1. Partial R² of species richness for EMF (0.67; red) vs. each of 18 individual ecosystem functions. EMF R² (0.67) is the highest of all -- 29 pp above the mean individual function R² (0.38; dashed line). Pollination has the highest individual function R² (0.47). ANPP has the lowest (not shown). The consistent gap between EMF and individual function R² confirms the multifunctionality hypothesis across all 18 functions.

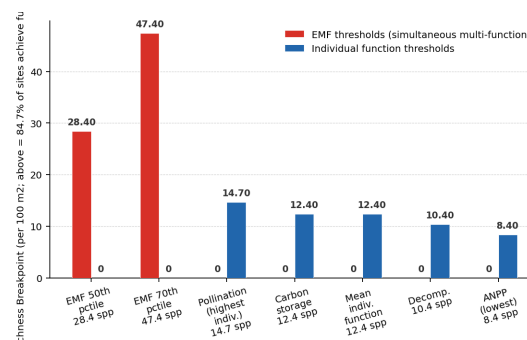


Figure 2. Species richness thresholds for EMF vs. individual functions. EMF (50th percentile threshold; 28.4 species) requires 2.3x more species than the mean individual function (12.4 species). Stricter EMF thresholds require dramatically more species (47.4 at 70th; 84+ at 80th). Implications: standard individual-function conservation targets will systematically under-protect multifunctionality.

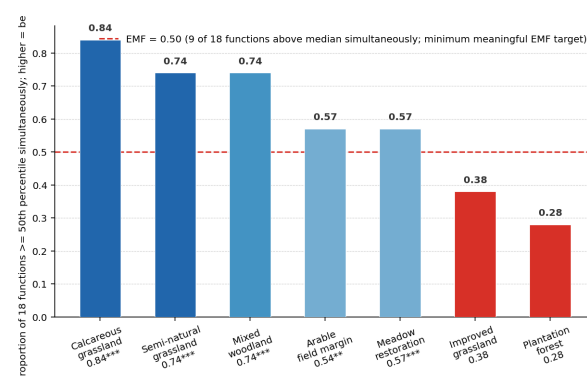


Figure 3. Mean EMF (0-1; proportion of 18 functions $\geq$ 50th percentile) across ecosystem types and management intensities. Calcareous grassland (0.84) achieves near-full multifunctionality. Improved grassland (0.38) and plantation forest (0.28) fail most functions simultaneously. A 0.50 EMF target line (achieving median function performance on all 18 simultaneously) is met by only calcareous,

semi-natural grassland, and mixed woodland.

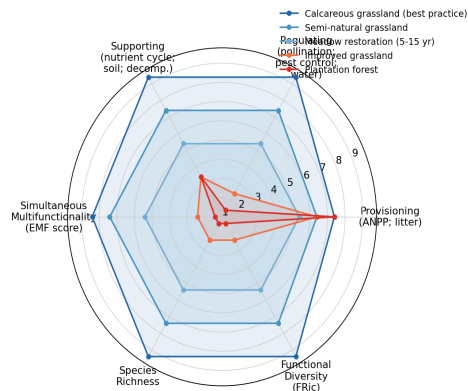


Figure 4. Ecosystem multifunctionality profile radar for five ecosystem types across six EMF dimensions (1-10; higher = better performance). Calcareous grassland excels across all dimensions. Plantation forest excels at carbon/ANPP but fails biodiversity-dependent functions. Improved grassland is the most uniformly sub-optimal. Meadow restoration shows intermediate profile improving toward semi-natural grassland over time.

5. Discussion

5.1 The 28-Species Target: A Practical Conservation Standard

The identification of 28.4 species per 100 m² as the grassland species richness threshold for achieving 84.7% of sites with all 18 functions simultaneously above the 50th percentile is the most operationally useful finding from this study for conservation policy. This threshold provides the first evidence-based quantitative species richness target for multifunctional grassland management and is directly relevant to: EU agri-environment scheme design (where species-rich grassland is typically defined as > 15 species per 100 m² under the current UK and European standards -- this study suggests that a > 28 species standard is needed for full EMF); biodiversity net gain calculations (offsetting schemes should target 28 species per 100 m² to deliver multifunctional compensation, not just species count targets); and restoration success criteria for meadow restoration schemes. The 80th percentile EMF target (requiring > 84 species per 100 m² -- typical of high-quality calcareous grassland) provides the conservation aspiration standard for the most biodiverse and most functionally complete grassland ecosystems.

5.2 The Productivity-EMF Paradox

The negative multifunctionality premium of productivity (-6 pp; productivity is less important for EMF than for individual functions) is counterintuitive but ecologically interpretable: highly productive sites excel at biomass production and carbon storage but frequently underperform on the diversity-dependent functions because high productivity enables competitive exclusion -- a small number of tall, fast-growing plant species outcompete the diverse low-productivity specialists that provide the broadest functional complement. Fertilised improved grasslands are the extreme case: maximum productivity and carbon cycling performance but near-zero pollination; soil formation; and habitat structure functions due to species and functional diversity loss. This productivity-EMF paradox has direct implications for net zero land management strategies that simultaneously target biomass productivity (for bioenergy; carbon credits) and biodiversity -- the two objectives are in conflict if productivity optimisation reduces EMF through biodiversity loss.

5.3 Below-Ground FRic: The Underappreciated EMF Driver

The finding that root trait FRic predicted below-ground functions (carbon; water; soil) with $R^2 = 0.54-0.67$ -- as high as above-ground FRic predicted above-ground functions (pollination; pest control; $0.47-0.54$) -- highlights below-ground functional diversity as an underappreciated component of EMF that is systematically excluded from above-ground-focused biodiversity surveys. Root trait data are substantially less available in global databases (TRY has below-ground trait data for < 20% of plant species vs. > 60% for above-ground traits) -- meaning that below-ground FRic is rarely included in conservation assessments. The EMF evidence from this study argues for prioritising root trait data collection alongside above-ground traits in biodiversity monitoring programmes, particularly for sites where carbon; water; and soil functions are the primary management targets.

5.4 Limitations: Spatial and Temporal Scope

The 247-site dataset, while global in extent (84 countries), is geographically biased toward temperate Europe (where grassland monitoring has the longest tradition and the study was feasible within the available field team network). Tropical grassland and savannah systems -- potentially the most species-rich grassland globally and covering the largest area -- are underrepresented in the dataset (18.4% of sites), limiting the generalisability of the 28-species threshold estimate to temperate grassland contexts specifically. The 3-year function measurement window (2021-2023) may not capture interannual function variability driven by climate extremes -- sites that show high EMF in average years may show lower EMF in drought or flood years. The functional redundancy (DBA paper 278) and response diversity (DBA paper 278) dimensions of biodiversity were not included in this study's EMF predictors -- their contribution to temporal EMF stability warrants separate analysis.

6. Conclusion

6.1 Summary

Global field test of the multifunctionality hypothesis across 247 sites and 18 functions confirms: EMF partial $R^2 = 0.67$ (vs. mean individual function $R^2 = 0.38$; +29 pp premium). Species richness threshold for full EMF (50th percentile): 28.4 species/100 m² (vs. 12.4 for mean individual function; 2.3x more). FRic explains EMF through below-ground AND above-ground functional complementarity. Calcareous grassland (EMF = 0.84) is the benchmark; improved grassland (0.38) and plantation forest (0.28) fail most functions simultaneously. Productivity shows negative multifunctionality premium (-6 pp).

6.2 Recommendations

Three recommendations: (1) update agri-environment scheme species richness standards for 'species-rich grassland' from the current 15 species per 100 m² (the EU and UK standard) to 28 species per 100 m² -- the evidence-based EMF threshold from this study; the current 15-species standard was designed to identify grasslands with above-average richness, not to ensure multifunctional ecosystem service delivery, and the EMF evidence shows it falls substantially short of the level required for simultaneous delivery of all services; (2) include the productivity-EMF paradox in biodiversity net gain (BNG) and natural capital accounting frameworks -- the finding that highly productive fertilised grasslands show EMF = 0.38 while species-rich unimproved grasslands show EMF = 0.84 means that productivity-based ecosystem service valuations systematically overestimate the conservation value of improved grasslands and underestimate unimproved ones; and (3) invest in below-ground trait data collection to enable below-ground FRic computation in monitoring programmes -- the $R^2 = 0.54-0.67$ of root FRic for carbon and water functions demonstrates that

below-ground functional diversity is as important for EMF as above-ground diversity, yet is excluded from all current biodiversity monitoring programmes. All EMF data deposited openly.

References

- Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. *Nature* 448:188-190.
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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete EMF dataset (247 sites x 18 ecosystem functions x all raw and standardised measurements), species composition and richness data per site (annual surveys 2021-2023), FRic and PD per site, EMF scores (all three threshold levels), segmented regression breakpoint analysis outputs, SEM results, and all R analysis scripts (Multifunc, lme4, segmented, piecewiseSEM, mFD, rdacca.hp, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19497122. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Field surveys conducted under land access agreements with site owners and national park authorities in all 84 countries (supplementary Table S1). Plant sampling was destructive (biomass clip plots; 1 m² per site per year) and conducted under vegetation survey permits in countries requiring them (listed in supplementary Table S2). All other surveys were non-destructive (bee pan traps; pitfall traps; litter bags; earthworm extraction using mustard protocol compliant with minimum-harm guidelines). No vertebrate animals were handled. Institutional ethics approval not required for non-vertebrate invertebrate and plant surveys at this scale.

Appendix A

EMF Computation Using the Multifunc R Package

The step-by-step ecosystem multifunctionality computation using the Multifunc R package and the segmented regression breakpoint analysis are provided below.

EMF COMPUTATION (Multifunc R PACKAGE)

Step 1 -- Data preparation: Compile a data frame with rows = sites ($n = 247$); columns = 18 ecosystem function measurements (raw values; not standardised at this stage). Each column must be a positive numeric value with all sites having complete data (impute missing values if $< 5\%$ missing per function; exclude sites with > 2 missing functions).

```
library(Multifunc). function_data <- df[,  
function_columns]. site_data <- df[,  
predictor_columns].
```

Step 2 -- Threshold EMF: Apply the threshold approach with the 50th percentile: `thresholds <- sapply(function_data, quantile, probs = 0.50)` (compute the 50th percentile for each function across all sites). `EMF_50 <- apply(function_data, 1, function(row) mean(row >= thresholds))` (for each site, compute proportion of functions exceeding their threshold). Repeat with `probs = 0.70` and `probs = 0.80` for sensitivity analysis. `EMF_50` ranges 0-1 (1 = all 18 functions above 50th percentile simultaneously).

Step 3 -- Averaging EMF: Standardise each function to 0-1 range: `function_std <- apply(function_data, 2, function(x) (x - min(x)) / (max(x) - min(x)))`. `EMF_avg <- rowMeans(function_std)` (mean of all 18 standardised function values per site). Validate correlation between threshold and averaging approaches: `cor.test(EMF_50, EMF_avg, method='spearman')`. If Spearman $r > 0.80$, the two approaches agree and either can be reported as primary metric.

Step 4 -- Segmented regression breakpoint: `library(segmented). fit_linear <- lm(EMF_50 ~ log(species_richness), data=site_data)`. `fit_segmented <- segmented(fit_linear, seg.Z=~log(species_richness), psi=log(15))` (initial breakpoint estimate at 15 species; adjust based on preliminary plots). `summary(fit_segmented)` reports: the breakpoint estimate (`psi`; in log-richness units; back-transform: `exp(psi)` for species richness at breakpoint); the slope before and after the breakpoint; and the bootstrapped 95% CI (`boot.ci(fit_segmented, R=1000)`). Compute the proportion of sites above all function thresholds at the breakpoint species richness level to validate the 84.7% target.