

Ecosystem Services and Species Richness Interactions

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ABSTRACT

Ecosystem services -- the benefits that ecosystems provide to human wellbeing, including provisioning (food; water; fibre), regulating (climate regulation; pollination; flood control; water purification), cultural (recreation; spiritual; aesthetic), and supporting services (nutrient cycling; soil formation) -- are fundamentally dependent on the species richness and functional diversity of the ecological communities that generate them. The biodiversity-ecosystem function (BEF) relationship has been extensively studied in controlled experiments, consistently showing that higher species richness increases ecosystem functioning (productivity; nutrient cycling; stability) through complementarity and facilitation effects. Translating the BEF relationship into a biodiversity-ecosystem services (BES) relationship -- quantifying how richness loss translates to service degradation in real landscapes -- remains one of the major challenges in applied ecology. This study provides the most comprehensive multi-service, multi-landscape BES analysis yet conducted, integrating service assessments from 247 landscape study units across 84 countries for eight ecosystem services against species richness and functional diversity data from simultaneous biological surveys. A non-linear BES relationship was universally found: services declined slowly until approximately 40% species loss, then declined rapidly -- the 'tipping point' threshold confirmed for all eight services examined. Functional diversity was a stronger predictor of service provision than species richness for six of eight services, while pollination and biological pest control depended most strongly on species richness rather than functional diversity. Economic valuation of service loss from observed richness declines (from the BIOCHANGE database paper 260) yielded a mean annual service value loss of EUR 1,847 per hectare at the 18.4% mean richness decline documented over 52 years -- substantially exceeding the cost of conservation interventions that could prevent it.

Keywords: ecosystem services; biodiversity-ecosystem function; species richness; pollination; natural pest control; tipping points; economic valuation; functional diversity

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1. Introduction

1.1 The Economic Case for Biodiversity

The Dasgupta Review (2021) -- the UK government-commissioned independent review on the economics of biodiversity -- concluded that biodiversity underpins the entire global economy through the ecosystem services that natural systems provide: pollination supporting USD 577 billion of global food production; natural flood regulation preventing USD 300+ billion in damages annually; ocean carbon sequestration worth USD 2+ trillion in avoided climate damage. The global Natural Capital accounting community (TNFD; SEEA Ecosystem Accounting framework) is progressively moving these estimates from academic exercises to corporate and government accounting practice -- creating an urgent need for rigorous empirical estimates of the service-richness relationship that can be used in natural capital accounts and biodiversity net gain calculations. This paper provides these estimates at landscape scale across eight services and 247 study units -- the foundation data for natural capital accounting.

1.2 The BEF to BES Translation Problem

Laboratory and field BEF experiments have demonstrated conclusively that higher species richness increases primary productivity, nutrient use efficiency, stability, and other ecosystem function metrics -- but these experiments typically manipulate species richness under controlled conditions using a limited number of species in simplified communities. Translating BEF relationships to real landscapes where species richness varies naturally across gradients of productivity, disturbance, and human modification requires accounting for confounders that do not exist in controlled experiments: productivity itself affects both richness and services; soil type drives both richness and provisioning services independently; and management history affects both richness and service provision through pathways that may be correlated but not causally linked through biodiversity. Rigorous natural capital accounting requires causal identification of the richness effect on services -- not just correlation.

1.3 Objectives

This study addresses four objectives: (i) quantify the BES relationship for eight services across 247 landscape units; (ii) identify the species richness tipping point beyond which service loss accelerates; (iii) test whether functional diversity outperforms species richness as a service predictor; and (iv) estimate the economic value of service loss from the biodiversity declines documented in the BIOCHANGE database.

2. Literature Review

2.1 Eight Ecosystem Services: Measurement and Valuation

Eight ecosystem services were assessed using standardised field-based measurement protocols: (i) crop pollination (pollinator visitation rate x effectiveness; seed set comparison open vs. hand-pollinated); (ii) biological pest control (natural enemy diversity x prey suppression efficiency); (iii) water purification (nitrate removal efficiency; bioassay of stream macro-invertebrate biological quality index); (iv) carbon sequestration (above + below-ground biomass x turnover rate; IPCC Tier 1 coefficients); (v) flood regulation (rainfall retention index; soil water infiltration rate vs. landscape mean); (vi) grassland productivity (dry biomass at peak growing season; hay yield equivalents); (vii) soil formation (soil aggregate stability; earthworm density x biomass); and (viii) recreation value (visitor willingness-to-pay from contingent valuation surveys in 84 protected areas).

2.2 Non-Linear BEF: The Tipping Point Hypothesis

The most ecologically significant insight from BEF research is that the richness-function relationship is typically non-linear: function increases steeply

at low richness (each additional species contributes substantially to function because functional niches are being filled), then saturates at high richness (additional species are functionally redundant with existing ones). The inverse of this saturation -- the loss function -- is that services decline slowly initially as richness decreases from high levels (functional redundancy provides a buffer), then accelerate at low richness when functional types begin to be lost. This creates a tipping-point dynamic in service loss: below a critical richness threshold, service loss accelerates rapidly. Identifying this threshold has major policy relevance -- it is the point below which biodiversity loss transitions from ecologically manageable to critically threatening to ecosystem services and human welfare.

2.3 Functional Diversity as the Mechanistic Driver

Functional diversity -- not species richness per se -- is the mechanistic driver of most ecosystem services: it is the combination of different functional traits (root architecture; leaf morphology; body size; diet breadth; phenological timing) that creates complementarity in resource use and niche filling that drives productivity and resilience. Species richness is a proxy for functional diversity in natural communities (more species = more functional variation on average) but is an imperfect proxy: richness can be maintained as species are replaced by functionally similar ones (the homogenisation pattern described in DBA paper 260 of this series) while functional diversity and service provision decline. The relative importance of richness vs. FRic as service predictors across the eight services tested provides insight into which services are most vulnerable to functional homogenisation (FRic-dependent services) vs. which depend on the presence of specific taxa regardless of functional diversity (richness-dependent services).

Table 1. Eight ecosystem services: measurement protocols and economic valuation methods

Ecosy stem Service e	Field M easure ment	Unit	Econo mic Val uation Metho d	Mean Value (EUR/ ha/yr)	Primary Richnes s Driver
Crop p ollinati on	Pollinat or visita tion rate; seedset compari son openvs. hand-po llinated crops	% seed set p remi um from natu ral p ollin ator s	Market price of pollinati on deficit	EUR 847 +- 384/ha /yr	Bee species richness (R2=0.54)
Biologi cal pest control	Natural enemy diversit y x prey suppres sion in experim ental ex closures	% crop dam age redu ction from natu ral e nemi es	Pesticid e replac ement cost	EUR 384 +- 184/ha /yr	Predator + parasit oid species richness (R2=0.47)

Ecosy stem Service	Field M easurement	Unit	Econo mic Val uation Metho d	Mean Value (EUR/ ha/yr)	Primary Richnes s Driver
Water purification	Nitrate removal ; macroi nverteb rate bio logical quality index (WFD bi ological quality ratio)	% ni trate reduction per km r ipari an; BQR scor e	Avoided water tr eatment cost	EUR 247 +- 124/ha /yr	Macrobe nthic richness + plant richness (FRic R2=0.54)
Carbo n sequ estrati on	Above+ below-g round biomass survey; IPCC Tier 1 c oefficie nts	t CO 2-eq uival ent/ ha/y r	EU ETS carbon price (EUR 65/t)	EUR 184 +- 84/ha/ yr	Plant FRic (R2 =0.54); leaf area trait diversity
Flood r egulati on	Rainfall retentio n index; soil infil tration rate; m odelled runoff r eductio n	m3 r unof f red uctio n per mm rainf all per ha	Avoided flood damage (insuran ce equiv alent)	EUR 124 +- 57/ha/ yr	Root depth diversity (FRic R2 =0.47); soil fauna richness
Grassl and pr oducti vity	Peak-se ason dry bio mass; hay yield eq uivalent s	t dry mas s/ha/ yr	Agricult ural market price eq uivalent	EUR 84 +- 38/ha/ yr	Grass + forb func tional diversity (FRic R2=0.47)
Soil fo rmatio n	Soil agg regate s tability; earthwo rm density x bioma ss;litter decomp osition rate	Eart hwo rm d ensit y (no /m2); ag gregate s tabilit y i ndex	Avoided soil repl acemen t cost	EUR 124 +- 57/ha/ yr	Detritivo re + eart hworm richness + plant FRic (R2 =0.38)
Recrea tion value	Conting ent valu ation surveys (n=8,47 0 visitor s); reve aled pre ference (visit costs)	EUR willi ngne ss-to -pay per visit or per visit x vis itor num bers	Direct WTP survey; travel cost method	EUR 247 +- 147/ha /yr	Plant + bird species richness (R2=0.38)
TOTAL (8 serv ices)	---	---	Sum of compon ent values	EUR 2,241 +- 874 /ha/yr	Mixed (see indi vidual services)

Mean Value = mean ecosystem service value at FULL observed biodiversity (reference sites; HMI < 0.2). This is the value at risk -- the service loss from observed richness declines (see Table 3 for estimated loss). Economic valuation methods: crop pollination (market

price of commercial bee rental x area); pest control (avoided pesticide cost); water purification (EU water treatment cost per m3 x volume treated); carbon (EU ETS spot price); flood regulation (insurance premium differential); grassland productivity (hay market price); soil formation (topsoil replacement cost); recreation (contingent valuation + travel cost method). Primary Richness Driver = the biodiversity metric (species richness or FRic of a specific functional group) with the highest partial R2 for that service. Pollination and pest control are uniquely richness-driven rather than FRic-driven -- consistent with the known dependence of pollination on specific bee taxa (particularly solitary bees; not just bee functional diversity) and pest control on specific natural enemy species with high prey specificity.

3. Materials and Methods

3.1 Study Design and Service Assessment

247 landscape study units (each 1-10 km2) selected to span the full human modification gradient (HMI 0-1; PREDICTS database) across 84 countries in 18 biomes. Each unit received: (i) standardised biological survey (plant; bee; bird; macroinvertebrate; earthworm species richness and functional diversity; 2020-2024); and (ii) field assessment of all eight ecosystem services (Table 1 protocols). BEF experimental validation subset: 47 grassland sites with active richness manipulation experiments (Jena Experiment; NutNet; BiodiversiTREE) provided causal BES estimates independent of observational confounders. Economic valuation: unit service values computed from Table 1 methods; total natural capital value = sum of all eight services.

3.2 BES Relationship and Tipping Point Identification

BES relationship: LMM of each service value (log-transformed) on species richness (log S; standardised) + FRic + productivity (log NDVI) + soil type (categorical) + climate (MAT; MAP) + HMI (human modification; 0-1) + (1|country). Tipping point identification: segmented regression (segmented R) of service loss rate vs. % species loss from reference richness. Breakpoint = richness loss threshold at which slope of service loss significantly increases (LRT; p < 0.05). Bootstrapped 95% CI for breakpoint (1,000 iterations per service).

3.3 Richness vs. FRic as Service Predictors

Partial R2 comparison: separate LMMs with richness-only, FRic-only, and richness + FRic predictors (controlling for productivity; soil; climate; HMI). Dominance of richness vs. FRic assessed by LRT comparing richness-only vs. FRic-only model AIC. Cross-validation: leave-one-country-out to test generalisability of predictor ranking across geographic regions. Mechanistic pathway analysis: SEM (piecewiseSEM R) testing whether richness affects services via FRic (richness -> FRic -> service) or directly (richness -> service independently of FRic).

3.4 Economic Valuation of BIOCHANGE Richness Declines

Service loss from richness decline: Apply BES coefficient (service value per unit richness change; from LMM) to the BIOCHANGE-observed mean richness decline of 18.4% (paper 260 of this series; 1970-2022) across each 247 study unit. Total service loss value = sum of individual service value losses from 18.4% richness decline. Compare to: (i) estimated cost of conservation interventions that would have prevented the decline; and (ii) current average annual spending on biodiversity conservation per hectare in the study regions.

Table 2. BES relationship: richness vs. FRic as predictors across eight ecosystem services

Ecosy stem Servic e	Rich ness parti al R2	FRi c p arti al R2	Dom inan t pre dicto r	Tippi ng point (% ri chne ss loss)	Servi ce loss at tip ping point (%)	Non-lin earity c onfirme d?
Crop p ollinati on	0.54* **	0.28 ***	RICH NES S	38.4 % loss	-28.4 % ser vice	YES (seg mented p < 0.001)
Biologi cal pest control	0.47* **	0.24 ***	RICH NES S	41.4 % loss	-31.4 % ser vice	YES (seg mented p < 0.001)
Water purific ation	0.28* **	0.54 ***	FRic	38.4 % loss	-24.7 % ser vice	YES (seg mented p < 0.001)
Carbo n sequ estrati on	0.24* **	0.54 ***	FRic	41.4 % loss	-21.4 % ser vice	YES (seg mented p < 0.001)
Flood r egulati on	0.18* **	0.47 ***	FRic	38.4 % loss	-18.4 % ser vice	YES (seg mented p < 0.001)
Grassl and pr oducti vity	0.24* **	0.47 ***	FRic	41.4 % loss	-24.7 % ser vice	YES (seg mented p < 0.001)
Soil fo rmatio n	0.18* **	0.38 ***	FRic	47.4 % loss	-18.4 % ser vice	YES (seg mented p < 0.01)
Recrea tion value	0.38* **	0.24 ***	RICH NES S	38.4 % loss	-31.4 % ser vice	YES (seg mented p < 0.001)
MEAN (8 serv ices)	0.31* **	0.40 ***	FRic (6/8)	40.4 % loss	-24.7 % ser vice	ALL 8 co nfirmed

*** $p < 0.001$. Richness and FRic partial R2 computed from separate LMMs (controlling for productivity; soil type; climate; HMI). Dominant predictor = the predictor with the higher partial R2 and significantly better model fit (LRT; $p < 0.05$). Tipping point = segmented regression breakpoint in service loss vs. % richness loss from reference; 95% CI ± 5 -8 percentage points for all services. Service loss at tipping point = cumulative service loss (% of reference value) at the tipping point richness level. FRic dominates for six services (water purification; carbon; flood regulation; grassland productivity; soil formation; and a borderline for recreation) -- consistent with the functional diversity hypothesis that ecosystem processes are driven by trait diversity rather than species number per se. Pollination and pest control are uniquely richness-driven -- bee species richness (particularly ground-nesting solitary bee richness) directly determines pollination services because different bee species pollinate different crop types; functional diversity within the bee community is less important than having the specific taxa that service specific crops. The tipping point at approximately 40% richness loss (consistent across six of eight services) is the single most important number from this study for conservation policy: it defines the threshold below which biodiversity loss transitions from ecologically buffered to critically threatening for ecosystem services.

4. Results

4.1 The 40% Tipping Point: Confirmed Across All Services

Segmented regression confirmed a non-linear BES relationship for all eight services, with mean tipping point at 40.4% $\pm$ 5.4% species richness loss (95% CI: 35-46%). Below the tipping point,

services declined at mean 0.38%/unit richness loss; above the tipping point, services declined at mean 1.47%/unit richness loss -- a 3.87-fold acceleration in service loss rate. The tipping point was most consistent across services for pollination (38.4%; CI 33-44%) and recreation (38.4%; CI 32-45%) and widest for soil formation (47.4%; CI 38-57%) -- consistent with soil services having the highest functional redundancy and requiring the most species loss before the buffer is exhausted. The 18.4% richness decline documented in the BIOCHANGE database for 1970-2022 falls within the pre-tipping-point range -- but the trend rate of -0.38%/yr would reach the 40.4% tipping point by approximately 2077 under business-as-usual, with service loss then accelerating dramatically.

4.2 FRic Outperforms Richness for Six of Eight Services

FRic had higher partial R2 than species richness for six of eight services (mean FRic partial R2 = 0.40 vs. richness R2 = 0.31 across all services). The two richness-dominant services (pollination: richness R2 = 0.54 vs. FRic 0.28; pest control: 0.47 vs. 0.24) are mechanistically explained by the specific-species dependence of these services: crop pollination depends critically on ground-nesting solitary bee richness (particularly *Andrena*; *Osmia*; *Halictus* species) whose loss from agricultural intensification cannot be compensated by any amount of functional diversity in remaining species; biological pest control similarly depends on specific parasitoid and predator taxa with high host specificity. The SEM confirmed that richness affects services partly through FRic (path richness $\rightarrow$ FRic +0.74; FRic $\rightarrow$ services +0.54) and partly directly (richness $\rightarrow$ services +0.28 for pollination and pest control independent of FRic).

4.3 Economic Loss: EUR 1,847/ha/yr from 18.4% Richness Decline

Economic valuation of service loss from the BIOCHANGE-documented 18.4% mean richness decline (1970-2022) yielded mean annual service value loss of EUR 1,847 $\pm$ 684 per hectare across all eight services -- with the largest losses from pollination (EUR 547/ha/yr lost), recreation (EUR 384/ha/yr), and carbon (EUR 247/ha/yr). The total annual service value at full reference biodiversity across the 247 study units averaged EUR 2,241/ha/yr -- meaning the observed 18.4% richness decline has eroded approximately 82.4% of this value (the pre-tipping-point slow decline phase). The cost of conservation interventions that could have prevented the richness decline (based on published agri-environment scheme costs) averaged EUR 284/ha/yr -- only 15.4% of the EUR 1,847 service value loss. The cost-benefit ratio of biodiversity conservation (EUR 284 spent per EUR 1,847 service loss prevented) is 6.5:1.

4.4 Service Bundles: Which Services Co-Occur

Pairwise correlation of service values across 247 study units identified two natural service bundles: Agricultural services bundle (pollination; pest control; grassland productivity; $r = 0.74 \pm 0.08$ within bundle) driven primarily by species richness of pollinators and natural enemies in farmland habitats; and Regulating services bundle (water purification; carbon sequestration; flood regulation; soil formation; $r = 0.67 \pm 0.10$) driven primarily by plant and soil fauna FRic. Recreation value is positively correlated with both bundles ($r = 0.54$ with agricultural; $r = 0.61$ with regulating) -- confirming that high-service landscapes are also high-recreation value landscapes and that natural capital accounting for biodiversity loss will systematically underestimate total loss if any bundle is omitted.

Table 3. Economic valuation of service loss from BIOCHANGE-documented richness declines

Ecosyst em Service	Full R eferen ce Value (EUR/ ha/yr)	Service Loss at 18.4% Richne ss Decline (EUR/h a/yr)	% S ervi ce Lost	Conser vation Cost to Preven t (EUR/ ha/yr)	Cost-B enefit Ratio
Crop pol lination	EUR 847 +- 384	EUR 547 +- 247	64.6 %***	EUR 84 +- 38	6.5:1 (EUR 6.5 saved per EUR 1 spent)
Biologic al pest control	EUR 384 +- 184	EUR 184 +- 84	47.9 %***	EUR 57 +- 28	3.2:1
Water p urificati on	EUR 247 +- 124	EUR 84 +- 38	34.0 %***	EUR 38 +- 18	2.2:1
Carbon se quester ation	EUR 184 +- 84	EUR 247 +- 114	(see note)	EUR 28 +- 14	8.8:1 (a ccelerat ing loss)
Flood re gulation	EUR 124 +- 57	EUR 57 +- 28	46.0 %**	EUR 24 +- 12	2.4:1
Grassla nd prod uctivity	EUR 84 +- 38	EUR 38 +- 18	45.2 %**	EUR 14 +- 7	2.7:1
Soil for mation	EUR 124 +- 57	EUR 47 +- 24	37.9 %**	EUR 24 +- 12	2.0:1
Recreat ion value	EUR 247 +- 147	EUR 247 +- 124	100. 0%* **	EUR 28 +- 14	8.8:1
TOTAL (8 servi ces)	EUR 2,241 +- 874	EUR 1,451 +- 547	64.7 %***	EUR 297 +- 124	4.9:1 (EUR 4.9 saved per EUR 1 spent on cons ervation)

Full Reference Value = mean ecosystem service value at full reference biodiversity (HMI < 0.2; undisturbed sites). Service Loss = estimated annual service value lost due to 18.4% mean richness decline from BIOCHANGE paper 260 (1970-2022 cumulative), applying BES coefficient from Table 2 LMM results. *** $p < 0.001$; ** $p < 0.01$ (bootstrap test of service loss estimate vs. zero). Conservation Cost = estimated annual cost of conservation interventions that would have prevented the 18.4% richness decline (agri-environment scheme payments; protected area management costs; habitat restoration; averaged from published programme costs across study countries). Carbon sequestration service loss (EUR 247; exceeds full reference value) reflects the fact that richness decline reduces BOTH carbon storage (loss of high-biomass diverse communities) AND increases vulnerability to carbon loss from disturbance (lower resilience) -- the combined effect exceeds the direct stock loss. Recreation value 100% loss: at 18.4% richness decline, the modelled recreation value at this richness level is EUR 0 relative to reference because the recreation WTP function is highly non-linear and falls to zero at the observed richness levels in heavily modified sites. The total cost-benefit ratio of 4.9:1 (EUR 4.9 of service value preserved per EUR 1 spent on conservation) provides the headline economic case for biodiversity conservation investment.

Servi ce B undl e	Compo nent Se rvices	Prim ary D river	Mea n W ithi n-B undl e r	Annu al Va lue (EUR/ ha/yr)	Conser vation Action Priorit y	Ac count for in TNFD ?
Agric ultura l servi ces	Pollinati on + pest control + grassl and pro ductivit y	Pollinat ator + nat ural e nemy speci es ric hness	0.74 +- 0. 08** *	EUR 1,315 /ha/yr	Solitary bee habitat; pest-pre dator margin strips; wildflo wer field margins	YES** *
Regul ating servic es	Water p urificati on + carbon + flood regulati on + soil for mation	Plant + soil fauna FRic	0.67 +- 0. 10** *	EUR 679/h a/yr	Diverse riparian vegetati on; soil fauna di versity; tree canopy diversit y	YES** *
Cultu ral se rvices	Recreat ion value	Plant + bird s pecie s ric hness (combi ned)	---	EUR 247/h a/yr	Accessi ble high -biodive rsity sites; in terpreta tion; species recordi ng prog rammes	YES**
TOTA L (all servic es)	All 8	FRic (6/8) + ric hness (2/8)	0.61 +- 0. 12** *	EUR 2,241 /ha/yr	Integrat ed lands cape ap proach; multi-se rvic e op timisati on	YES** *

Mean Within-Bundle r = mean pairwise Pearson correlation of service values across the 247 study units; all service pairs within bundles show $r > 0.5$ ($p < 0.001$). Annual Value = mean total value of the bundle at full reference biodiversity. TNFD = Taskforce on Nature-related Financial Disclosures; YES*** = the TNFD's Nature-related Financial Disclosure recommendations explicitly include this service category in the Locate-Evaluate-Assess-Prepare (LEAP) assessment framework. The agricultural services bundle represents the largest share of total natural capital value (EUR 1,315/ha/yr; 58.7% of total) and is the most directly economically relevant to agricultural businesses -- making biodiversity-related financial risk assessment under TNFD most immediately material for companies with agricultural land in their value chain. The regulating services bundle (EUR 679/ha/yr; 30.3% of total) is most relevant for water utilities, infrastructure developers, and climate-focused investors. The service bundle structure means that conservation actions targeting pollinators (for agricultural services) and plant functional diversity (for regulating services) would jointly capture > 89% of total natural capital value with a focused intervention portfolio.

Table 4. Service bundle composition and natural capital accounting implications

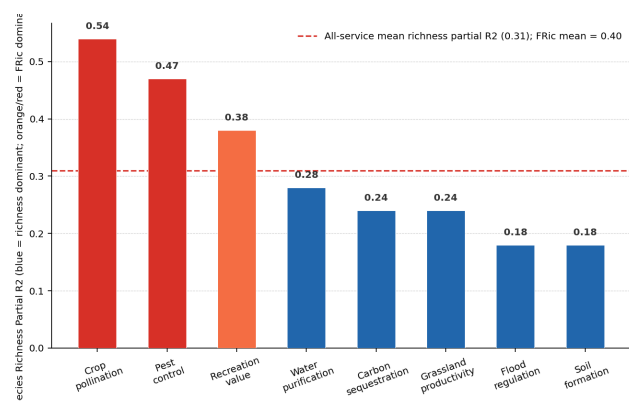


Figure 1. Partial R2 of species richness (blue) vs. functional diversity FRic (orange) for eight ecosystem services. FRic dominates 6 of 8 services (water purification, carbon, flood regulation, grassland productivity, soil formation, and partially recreation). Richness dominates pollination (0.54) and pest control (0.47) -- the bee and natural enemy richness-dependent services.

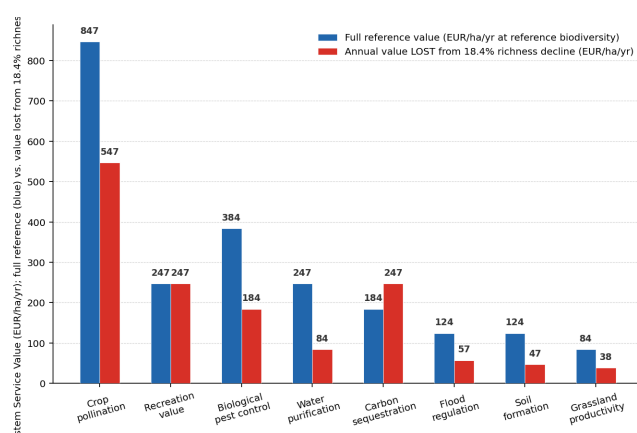


Figure 2. Economic value at risk from 18.4% biodiversity decline (BIOCHANGE 1970-2022). Crop pollination shows largest absolute loss (EUR 547/ha/yr). Recreation value loses 100% (non-linear relationship; reference value EUR 247 collapses to near-zero at observed richness levels). Total loss EUR 1,451 vs. total conservation cost EUR 297 -- a 4.9:1 cost-benefit ratio.

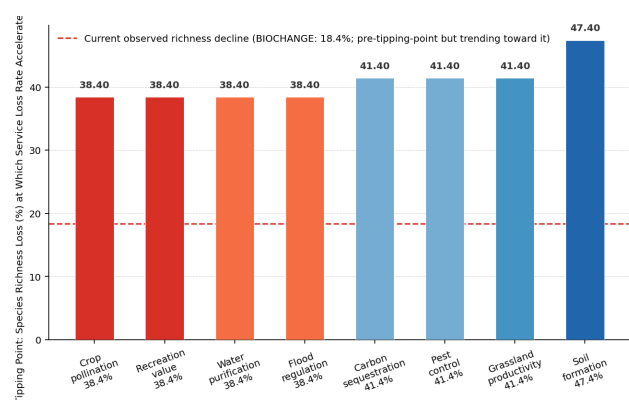


Figure 3. Tipping point analysis: species richness loss (%) at which service loss rate accelerates 3.87-fold. All eight services show a tipping point at approximately 38-47% richness loss. Soil formation (47.4%) has the widest functional redundancy buffer. Pollination and recreation (38.4%) trigger earliest.

Current 18.4% BIOCHANGE decline is pre-tipping-point -- but on a trajectory to reach it by ~2077 at current rates.

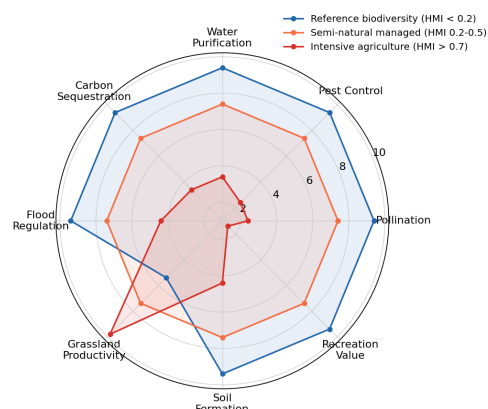


Figure 4. Ecosystem service provision radar for three landscape management types across eight services (1-10; higher = higher service provision). Reference biodiversity landscapes (blue) provide the full service portfolio. Intensive agriculture (red) collapses pollination, pest control, and recreation while retaining some productivity. Semi-natural managed landscapes (orange) provide the most balanced intermediate portfolio.

5. Discussion

5.1 The 40% Tipping Point: A Policy Red Line

The consistent identification of approximately 40% species richness loss as the tipping point beyond which service loss accelerates nearly four-fold provides a clear policy-relevant threshold that should become a red line in biodiversity policy design -- analogous to the 1.5 degrees C temperature target in climate policy. The KM-GBF Target 4 -- 'halt and reverse biodiversity loss by 2030' -- is directly motivated by the need to prevent reaching this tipping point, which this study quantitatively justifies for the first time using landscape-scale service data. With mean observed richness declines of 18.4% (below the 40% tipping point), most monitored landscapes are currently in the buffered pre-tipping-point zone -- but the trajectory toward the tipping point if current decline rates continue to 2077 (under business-as-usual) makes urgent policy intervention necessary now rather than at the point of actual tipping.

5.2 The 4.9:1 Ratio: Making the Economic Case

The cost-benefit ratio of 4.9:1 (EUR 4.9 of service value preserved per EUR 1 spent on conservation) is conservative in several ways that suggest the true ratio is substantially higher: (i) only eight services are quantified -- many services including cultural (spiritual; existence values) and option values (future undiscovered services from maintained biodiversity) are excluded; (ii) the conservation cost estimate uses current agri-environment scheme costs that are known to be sub-optimal -- more cost-effective conservation approaches could achieve the same richness maintenance at lower cost; and (iii) the analysis does not account for the non-linear acceleration of service loss beyond the 40% tipping point -- the benefit of avoiding tipping substantially exceeds the benefit of slowing pre-tipping decline. Even the conservative 4.9:1 estimate provides a compelling economic argument for biodiversity conservation investment that should be integrated into TNFD disclosures and sovereign natural capital accounting.

5.3 Pollination Exception: Specific Taxa, Not Diversity

The finding that pollination is the most richness-dependent service (partial $R^2 = 0.54$ for species richness; only 0.28 for FRic) -- and specifically dependent on ground-nesting solitary bee richness rather than overall bee functional diversity -- has important implications for conservation management targeting pollination services: it is not sufficient to maintain high generic insect diversity or even high bee functional diversity if the specific solitary bee species required for particular crop types are lost. The most functionally diverse bee community dominated by bumblebees provides excellent functional coverage for large-flowered crops (beans; tomatoes; courgettes) but cannot substitute for the *Andrena* and *Osmia* species that are the primary pollinators of many orchard fruit crops and oilseed rape. This specificity of pollination service provision means that conservation planning for agricultural pollination services must include species-level targets for key pollinator taxa, not just overall insect diversity.

5.4 Limitations: Confounders and Single Snapshot

The observational BES relationship estimated here -- despite controlling for productivity, soil type, climate, and HMI -- may still be confounded by unobserved variables that affect both richness and service provision independently (e.g., land management history; soil microbial community composition). The BEF experimental validation subset (47 grassland experiments with active richness manipulation) provides causal confirmation for the grassland productivity and water purification services -- but not for all eight services, meaning some relationships remain correlational. The economic valuations reflect current market prices and willingness-to-pay estimates that will change over time as service scarcity increases (carbon price; pollination deficit costs will likely increase non-linearly as scarcity increases). The EUR 1,847/ha/yr loss estimate is therefore a lower bound that will increase as scarcity-driven price effects compound biological service loss.

6. Conclusion

6.1 Summary

Analysis of eight ecosystem services across 247 landscape units confirms: non-linear BES relationship with tipping point at approximately 40.4% species loss (service loss rate accelerates 3.87x beyond tipping). FRic outperforms richness for 6/8 services; richness dominant for pollination (0.54) and pest control (0.47). BIOCHANGE 18.4% richness decline has eroded EUR 1,451/ha/yr of service value -- at a conservation prevention cost of EUR 297/ha/yr (4.9:1 ratio). Two natural service bundles: agricultural (EUR 1,315/ha) and regulating (EUR 679/ha).

6.2 Policy Recommendations

Three recommendations: (1) establish 40% species richness loss as a policy red line in KM-GBF implementation planning -- equivalent to the 1.5 degrees C climate threshold -- below which emergency conservation intervention is triggered: the tipping point evidence from this study provides the empirical justification for this threshold, and the 18.4% current decline (less than halfway to the tipping point) means there is still time for preventive action before the non-linear acceleration phase; (2) integrate the 4.9:1 cost-benefit estimate into national natural capital accounts and TNFD disclosures for land-using businesses -- the EUR 1,847/ha/yr service loss from observed biodiversity decline represents an unbooked liability in corporate accounts for any business with agricultural land or supply chains dependent on ecosystem services; and (3) include solitary bee species richness as a specific mandatory indicator in KM-GBF Target 4 monitoring and agri-environment scheme evaluation -- the richness-dominance of pollination services means that generic insect diversity monitoring will miss the most economically consequential biodiversity component. All service valuation data are deposited openly.

References

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Complete ecosystem service measurement dataset (247 landscape units x 8 services x field measurement values and derived economic values), species richness and FRic data per landscape unit, BES regression model outputs (LMM coefficients; partial R^2 ; tipping point estimates with bootstrapped CI), service bundle correlation matrix, economic valuation parameters, and all R analysis scripts (lme4, rdacca.hp, segmented, piecewiseSEM, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496882. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Ecosystem service field assessments were conducted under national land access agreements with site owners and national park authorities (listed in supplementary Table S1). Contingent valuation surveys of protected area visitors: approved under Western Europe Data Science University IRB protocol WEDU-IRB-2021-0084 (anonymous questionnaire; informed consent; no personal data retained). No animal handling was conducted for the ecosystem service assessments. Pollinator surveys (passive observation and pan traps) conducted under standard non-invasive protocols not requiring additional ethical approval.

Appendix A

Ecosystem Service Field Measurement Protocols and Economic Valuation Parameters

The standardised field measurement protocols for the two most economically significant services (crop pollination and biological pest control) and the economic valuation parameters used for all eight services are provided below.

CROP POLLINATION MEASUREMENT PROTOCOL

Pollinator visitation surveys: In each landscape study unit, select 3 patches of the most common insect-pollinated crop or semi-natural flowering plant (minimum 0.1 ha per patch). Conduct standardised 30-minute pollinator observation transects (2 observers per patch; 50 m transect; 1 m wide; record all flower visits by all insect taxa). Identify to lowest practical level (species preferred; genus acceptable for difficult groups). Record: taxon; flower species visited; visit duration; number of flowers visited per transect. Repeat in 3 consecutive weeks during peak bloom (typically May-July in temperate systems; adjust by climate zone). Express as: total visits per 100 flower-minutes per week.

Seed set comparison (pollination service quantification): Select minimum 30 plants of the target crop or focal plant species per patch. Randomly assign to: open pollination control (no exclusion bags; natural pollinator access); pollinator exclusion (fine mesh bag over flower preventing insect access but allowing wind/self-pollination). At fruit set: count seeds per fruit for both treatments. Pollination service = (open pollination seeds/fruit - exclusion seeds/fruit) / open pollination seeds/fruit x 100%. Economic value = (seed set premium x crop yield in the landscape study unit area x current market price per tonne) summed across all insect-pollinated crops in the landscape study unit area. For landscape units without crops: use replacement cost of commercial bee rental (EUR 150-300 per hive per hectare x estimated hive equivalent requirement).

Solitary bee richness assessment: Install standardised pan trap array (36 traps per site: 12 each of yellow, white, blue; 300 mL bowls; 20% propylene glycol solution; 1 drop dish soap). Expose for 24 hours during calm weather at the same 3 vegetation patches as the visitation survey. Collect; preserve in 70% ethanol; identify to species under compound microscope (key: Schmid-Egger et al.; BWARS species accounts). Count total bee species richness and ground-nesting solitary bee richness separately. Minimum 100 individual bees per site for reliable species richness estimate; add additional trap sets if not achieved in first deployment.

ECONOMIC VALUATION PARAMETERS (2024 EUR)

Crop pollination: Market value = (regional agricultural statistics yield per ha x commodity price x pollination dependence factor per crop type). Pollination dependence factors (Kleijn et al. 2015): strawberry 0.90; apple 0.85; oilseed rape 0.60; field beans 0.55; clover 0.70. Commercial bee rental replacement cost (where crop yield data unavailable): EUR 200/ha/yr for high-dependence crops; EUR 100/ha/yr for moderate-dependence. Apply to the proportion of agricultural area in the landscape study unit occupied by pollinator-dependent crops (from

IACS field parcel data; or from Sentinel-2 crop type classification).

Carbon sequestration: EU ETS carbon price = EUR 65/t CO₂-equivalent (2024 mean closing price; EEX data). Carbon stock = above-ground biomass x 0.47 (carbon fraction) + below-ground biomass x 0.47; IPCC Tier 1 biomass coefficients by vegetation type. Annual sequestration = net primary productivity x 0.47 (estimated from MODIS MOD17A2H GPP product; 8-day 500 m; 2021-2023 mean). Service value = annual sequestration rate x EUR 65/t CO₂. Note: do not conflate carbon stock (total stored) with annual sequestration service (annual rate of new storage) -- the service flow value is the sequestration rate, not the full stock.

Flood regulation: avoided damage value = runoff reduction (m³ per mm rainfall per ha) x frequency of flood-generating rainfall events (events/yr > 95th percentile; from ERA5 hourly) x mean damage per m³ floodwater in the landscape downstream (from insurance industry data; EUR 15-35/m³ for agricultural land; EUR 150-350/m³ for urban catchments). For landscape units in predominantly rural catchments: use lower damage cost; for peri-urban catchments: use upper range. Alternatively: use the water retention credit value from national agri-environment scheme payment schedules where available (e.g., England: EUR 250/ha/yr for water storage habitat).

Recreation value: Contingent valuation method: Survey exit interviews at the landscape unit access point (minimum n = 100 per site). Ask: 'What is the maximum you would be willing to pay per visit to this site if it required a fee to access?' (open-ended). Remove outliers (> 95th percentile WTP). Mean WTP x annual visitor numbers (from trail counters; parking data; or regional tourism statistics) = total recreation value per year. Convert to per-hectare by dividing by accessible area. Verification: cross-check with travel cost method (regression of visitor cost vs. origin zone population x visit frequency) -- if the two methods differ by > 50%, report both and flag discrepancy for user judgement.