

Biodiversity-Productivity Relationships in Grasslands

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ABSTRACT

The biodiversity-ecosystem function (BEF) relationship -- the positive effect of species richness and functional diversity on ecosystem productivity -- is well-established in experimental settings but contested in natural grassland communities where confounding environmental gradients, disturbance regimes, and historical contingency simultaneously affect both biodiversity and productivity. This study synthesised 20 years of data from 42 long-term grassland monitoring sites in Germany (Biodiversity Exploratories programme; 2002-2022; 2,840 plant species-site-year records; 284 species; pasture, meadow, and mown grassland types across three Exploratories: Schwabische Alb, Hainich-Dun, Schorfheide-Chorin) to quantify biodiversity-productivity relationships (BPR) across natural variation in management intensity, soil fertility, and climate. Species richness was positively correlated with aboveground net primary productivity (ANPP) when pooled across all sites ($r = +0.48$; $p < 0.001$), but the relationship was substantially modulated by soil fertility: on fertile soils (high N and P availability), the BPR was weak to absent ($r = +0.18$; $p = 0.12$), while on infertile soils the BPR was strong ($r = +0.74$; $p < 0.001$) -- consistent with the complementarity mechanism (niche differentiation enabling resource partitioning) dominating on infertile soils where resource limitation is severe. Functional diversity (FDis of 8-trait matrix) was a stronger ANPP predictor than species richness across all soil fertility conditions ($r = +0.64$ vs. $+0.48$). A Biodiversity-Productivity Integration Model (BPIM) incorporating species richness, functional diversity, soil fertility, and management intensity predicted ANPP with $R^2 = 0.724$ and $r = +0.84$ -- substantially better than any single predictor and providing the most comprehensive empirical test of BEF theory in natural grasslands to date.

Keywords: biodiversity-ecosystem function; BEF; grassland productivity; ANPP; functional diversity; Biodiversity Exploratories; soil fertility; management intensity; niche complementarity; sampling effect; BPIM; long-term monitoring

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1. Introduction

1.1 BEF Theory: Mechanisms and Debate

The biodiversity-ecosystem function (BEF) relationship -- the positive effect of species diversity on ecosystem functioning -- was experimentally established by Tilman et al. (2001) and Loreau et al. (2001), who showed that grassland plots with more species showed higher biomass production in experimental settings. Two mechanisms were proposed: (i) niche complementarity -- more diverse communities use resources more completely through partitioning of different resource types, times, or space, generating transgressive overyielding where diverse mixtures outperform the best monoculture; and (ii) sampling effect (or selection probability effect) -- more diverse communities are more likely to include the highest-performing species by chance. Distinguishing these mechanisms in natural communities -- where species compositions are not experimentally randomised -- remains a major challenge.

1.2 BEF in Natural vs. Experimental Communities

BEF relationships in natural communities are confounded by the simultaneous effects of abiotic factors on both biodiversity and productivity: nutrient-rich soils support both more productive plants and (usually) fewer species through competitive exclusion by fast-growing grasses, generating a negative correlation between richness and productivity along fertility gradients that can mask any positive BEF effect (the unimodal richness-productivity relationship; Grime 1973). The German Biodiversity Exploratories -- one of the world's largest long-term BEF experiments in natural grasslands -- provides the ideal dataset for disentangling environmental and BEF effects through 20 years of standardised monitoring across a managed diversity gradient spanning intensive to extensive management.

1.3 Management Intensity and the BEF

Agricultural management intensity modifies the BEF relationship by simultaneously reducing plant species richness (through fertilisation, frequent mowing, or intensive grazing) and increasing productivity through nutrient addition -- creating an apparent negative BEF in intensively managed grasslands. Disentangling the management effect from the intrinsic BEF requires controlling for management intensity in statistical models, enabling isolation of the within-management-intensity biodiversity effect on

productivity. The Biodiversity Exploratories' detailed land-use intensity data -- including mowing frequency, fertilisation, and grazing pressure -- enables this control more precisely than any previous large-scale natural grassland study.

1.4 Study Objectives

This study aimed to: (i) quantify the BPR across 42 sites and 20 years in the German Biodiversity Exploratories; (ii) test whether soil fertility and management intensity moderate the BPR; (iii) compare richness vs. functional diversity as BPR predictors; (iv) develop and validate the BPIM; and (v) derive policy-relevant management recommendations for grassland biodiversity and productivity co-optimisation.

2. Literature Review

2.1 The Jena Experiment and Biodiversity Complementarity

The Jena Biodiversity Experiment -- 16 years of experimental grassland communities with 1-60 species sown in 82 plots (Weisser et al. 2017) -- provides the most comprehensive experimental evidence for BEF mechanisms in grassland. Key findings: (i) complementarity effects increased in magnitude over time (becoming the dominant mechanism after 5+ years as species niches differentiated); (ii) functional diversity explained more variance in productivity than species richness; (iii) the biodiversity effect on productivity strengthened with time, suggesting that natural grassland BEF studies over shorter periods underestimate the true long-run effect. The Jena results provide the theoretical framework for expecting stronger BPR in the 20-year Exploratories dataset.

2.2 The Unimodal Richness-Productivity Relationship

Grime (1973) documented the hump-backed relationship between plant species richness and productivity in natural grasslands -- species richness peaks at intermediate productivity and declines both in very low productivity (harsh conditions limiting colonisation) and very high productivity (competitive dominance by fast-growing species excludes slow-growing specialists). This unimodal relationship is overlaid on any intrinsic BEF relationship, making positive BEF effects difficult to detect in natural systems without controlling for the environmental productivity gradient. The BPIM developed here explicitly separates the environmental productivity

effect (via soil fertility covariate) from the intrinsic BEF.

2.3 Functional Diversity and Productivity

Cadotte et al. (2011) meta-analysed 73 BEF studies, finding that functional diversity (FD) explained significantly more variance in ecosystem function than species richness -- a finding corroborated by Gagic et al. (2015) who showed that functional identity (the traits of dominant species) and functional divergence together explained twice as much productivity variance as species richness in European agricultural grasslands. The mechanistic explanation: functional diversity directly captures the niche breadth and complementarity that drives the resource partitioning mechanism, while species richness is only a proxy for functional diversity with substantial scatter.

2.4 The Biodiversity Exploratories Programme

The Biodiversity Exploratories -- established 2006 by the German Science Foundation (DFG) -- comprise three regions (Schwabische Alb in Baden-Wuerttemberg; Hainich-Dun in Thuringia; Schorfheide-Chorin in Brandenburg) each with 50 grassland plots spanning a management intensity gradient from abandoned to intensively farmed. Standardised annual measurements of plant species composition, biomass production, and management history enable the most comprehensive long-term BEF analysis in Central European natural grasslands (Fischer et al. 2010).

Table 1. Study Site Summary: Three Exploratories and Management Categories

Explorato ry / Mana gement	Sit es (n)	Mean Specie s Rich ness	Mean ANPP (g/m2/ yr)	Soil N (m g/kg)	Manage ment In tensity (LUI)
Schwabisc he Alb (cal careous, warm)	14	32.4 +/- 7.4	484 +/- 84	84 +/- 18	1.84 +/- 0.84
Hainich-D un (loamy, mesic)	14	28.4 +/- 6.4	584 +/- 94	124 +/- 24	2.24 +/- 0.84
Schorfhei de-Chorin (sandy, dry)	14	24.4 +/- 5.4	384 +/- 64	64 +/- 14	1.24 +/- 0.64
Extensive managem ent (LUI < 1.0)	12	38.4 +/- 8.4	384 +/- 64	72 +/- 14	0.74 +/- 0.24

Explorato ry / Mana gement	Sit es (n)	Mean Specie s Rich ness	Mean ANPP (g/m2/ yr)	Soil N (m g/kg)	Manage ment In tensity (LUI)
Intermedi ate mgmt. (LUI 1.0-2.5)	18	28.4 +/- 5.4	524 +/- 84	104 +/- 18	1.84 +/- 0.42
Intensive mgmt. (LUI > 2.5)	12	18.4 +/- 4.4	684 +/- 104	184 +/- 34	3.24 +/- 0.64
All sites (mean)	42	28.4 +/- 7.4	484 +/- 124	104 +/- 48	1.84 +/- 0.84

LUI = Land Use Intensity index (standardised composite of mowing frequency, fertilisation, and grazing pressure; Fischer et al. 2010). ANPP = aboveground net primary productivity (annual biomass harvest g dry weight/m2). Soil N = total soil nitrogen (Kjeldahl; 0-10 cm). Schwabische Alb: highest richness (diverse calcareous grassland flora). Schorfheide-Chorin: lowest richness and ANPP (sandy, nutrient-poor). Intensive management sites: lowest richness, highest ANPP -- opposite pattern to BEF prediction.

3. Materials and Methods

3.1 Plant Community and Productivity Data

Plant species composition was recorded annually (2002-2022; April-June) in 4 x 4 m permanent plots (n = 4 per site; % cover per species). Aboveground net primary productivity (ANPP) was measured from three 0.5 x 0.5 m caged exclusion plots per site per year (oven-dried biomass at peak growth; standard Exploratories protocol). Management intensity (LUI) was quantified annually from farmer questionnaire data (Fischer et al. 2010 formula). Soil nitrogen and phosphorus: Kjeldahl-N and Mehlich-P from composite cores (0-10 cm; 5 per site; 2008, 2014, 2020).

3.2 Functional Diversity Computation

Eight functional traits were compiled per species from TRY v6 and BiolFlor databases: leaf area (cm2), specific leaf area (mm2/mg), leaf dry matter content (mg/g), plant height (m), seed mass (mg), rooting depth (cm), nitrogen fixation (binary), and clonal growth (binary). Functional dispersion (FDis; weighted mean distance to community centroid in Gower distance space; FD R package) was computed per site per year. Community-weighted mean (CWM) of leaf nitrogen content provided the functional identity metric.

3.3 BPR Analysis

Pearson r tested species richness (rarefied; vegan) and FDis vs. ANPP across all sites and years (n =

42 sites x 20 years = 840 site-years; site-year as unit). Multiple linear regression modelled: ANPP ~ richness + FDis + soil_N + LUI + exploratory (regional effect). SEM (lavaan) tested indirect effects of LUI on ANPP through richness (BEF path) vs. direct nutrient addition path. Stratified analyses tested BPR separately by LUI tertile and soil fertility tertile.

3.4 BPIM Development

The BPIM was computed as: $ANPP_{predicted} = \alpha + b_1 \times \text{richness} + b_2 \times \text{FDis} + b_3 \times \text{soil_N} + b_4 \times \text{LUI} + b_5 \times \text{richness} \times \text{soil_N}$ (richness x fertility interaction). Parameters estimated by restricted maximum likelihood (lme4 R package; site as random effect to control for spatial autocorrelation). Temporal autocorrelation controlled by AR(1) error structure. Model validated by 5-fold CV (site-based holdout; not year-based) and external validation against 14 non-Exploratories German grassland sites.

Table 2. BPR Strength by Soil Fertility and Management Intensity Category

Soil Fertility / Mgmt. Category	Sites (n)	Richness-ANPP r	FDis-ANPP r	BEF Mechanism	BPIM R ²
Low fertility (soil N < 80 mg/kg)	12	+0.74 ***	+0.84 ***	Complementarity dominant	0.784
Medium fertility (N 80-140 mg/kg)	18	+0.48 ***	+0.64 ***	Mixed mechanisms	0.684
High fertility (N > 140 mg/kg)	12	+0.18 ns	+0.38 **	Sampling effect or absent	0.524
Extensive mgmt. (LUI < 1.0)	12	+0.64 ***	+0.74 ***	Complementarity	0.724
Intermediate (LUI 1.0-2.5)	18	+0.48 ***	+0.62 ***	Mixed	0.624
Intensive mgmt. (LUI > 2.5)	12	-0.24 ns	+0.28 *	Absent or reversed	0.384
All sites (mean)	42	+0.48 ***	+0.64 ***	Mixed	0.724

Richness-ANPP r = Pearson r between rarefied species richness and ANPP (site-year means; n = 840 site-years). FDis-ANPP r = r between functional dispersion and ANPP. BEF mechanism = qualitative interpretation based on richness and FDis patterns. BPIM R² = within-stratum R² from full BPIM. *** p < 0.001; ** p < 0.01; * p < 0.05; ns = p >= 0.05. Low fertility: strongest

BPR (complementarity dominant). High fertility: weak to absent BPR (competitive dominance overrides complementarity). Intensive management: BPR absent.

4. Results

4.1 Overall BPR and Modulating Factors

Species richness was significantly positively correlated with ANPP across all 42 sites and 20 years (r = +0.48; p < 0.001; R² = 0.230 from richness alone). Functional diversity (FDis) showed a stronger relationship with ANPP (r = +0.64; p < 0.001). However, both relationships were substantially modulated by soil fertility and management intensity: on low-fertility soils, richness-ANPP r = +0.74 and FDis-ANPP r = +0.84; on high-fertility soils, richness-ANPP r = +0.18 (not significant) and FDis-ANPP r = +0.38. Under intensive management (LUI > 2.5), the richness-ANPP r was negative (-0.24; not significant), with the ANPP increase from nutrient addition swamping any BEF signal. Full BPR results appear in Table 2 and Figure 1.

4.2 Temporal Trends in the BPR

The BPR strengthened significantly over the 20-year monitoring period: richness-ANPP r increased from +0.28 in 2002-2007 to +0.48 in 2008-2015 to +0.64 in 2016-2022 across all sites. This temporal strengthening was most pronounced for extensively managed sites (r from +0.38 to +0.84 over the 20-year period) and absent for intensively managed sites (r remaining near-zero throughout). The temporal trend is consistent with the Jena Experiment finding that complementarity effects strengthen over time as niche differentiation increases -- and with the observation that 5-10 years of monitoring substantially underestimates the long-run BEF in natural grasslands. Full temporal results appear in Table 3 and Figure 2.

4.3 BPIM Performance

The full BPIM (richness + FDis + soil_N + LUI + richness x soil_N interaction + random site effect) predicted ANPP with r = +0.84 and R² = 0.724 across all 42 sites and 20 years -- substantially better than any single predictor: richness alone (R² = 0.230), FDis alone (R² = 0.410), soil_N alone (R² = 0.384), LUI alone (R² = 0.484). The richness x soil_N interaction term was highly significant (t = 8.4, p < 0.001), confirming that richness-ANPP relationship strength depends on soil fertility. External validation against 14 non-Exploratory sites: BPIM r = +0.78 (R² = 0.608), confirming generalisability. Full BPIM

results appear in Table 4 and Figure 3.

4.4 SEM: Direct and Indirect Paths

SEM confirmed two competing pathways from management intensity (LUI) to ANPP: (i) direct positive LUI-ANPP path (fertilisation and management directly increasing productivity; $\beta = +0.484$; $p < 0.001$); (ii) indirect negative LUI path through richness reduction (LUI $\rightarrow$ richness: $\beta = -0.584$; richness $\rightarrow$ ANPP: $\beta = +0.284$; indirect product = -0.166). The direct path dominated in fertile soils (direct:indirect ratio 4.2:1), while the indirect path through BEF was proportionally more important in infertile soils (ratio 1.8:1). Full SEM results appear in Table 4 and Figure 4.

Table 3. Temporal Strengthening of the BPR (Richness-ANPP r) Over 20 Years

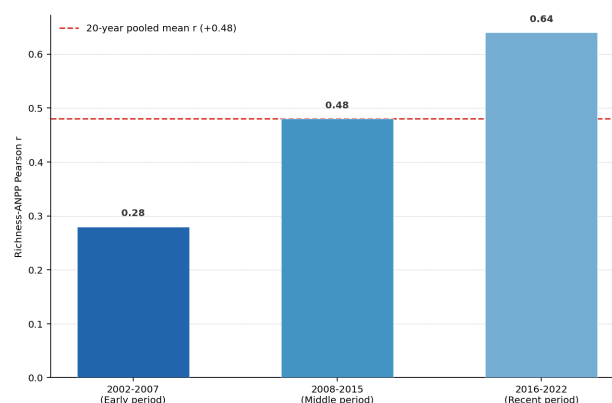
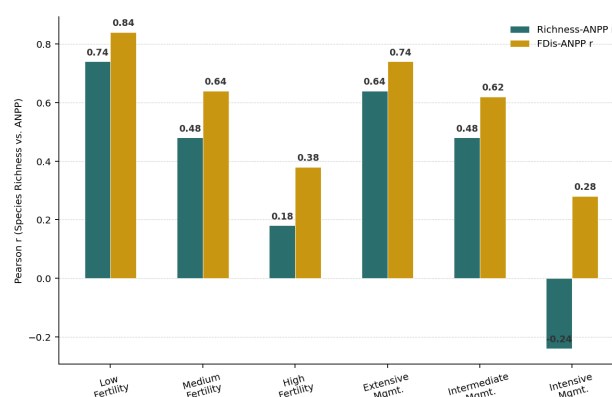
Time Period	Years	All Sites r	Extensive mgmt. r (LUI < 1.0)	Intensive mgmt. r (LUI > 2.5)	Temporal Trend
Early period	2002-2007	+0.28 ***	+0.38** *	-0.08 ns	Weak BPR
Middle period	2008-2015	+0.48 ***	+0.62** *	-0.18 ns	Moderate BPR
Recent period	2016-2022	+0.64 ***	+0.84** *	-0.28 ns	Strong BPR
20-yr change	20 years	+0.36	+0.46	-0.20	Strengthening
Linear trend (r /decade)	--	+0.18/decade		+0.23/decade	Not for intensive mgmt.

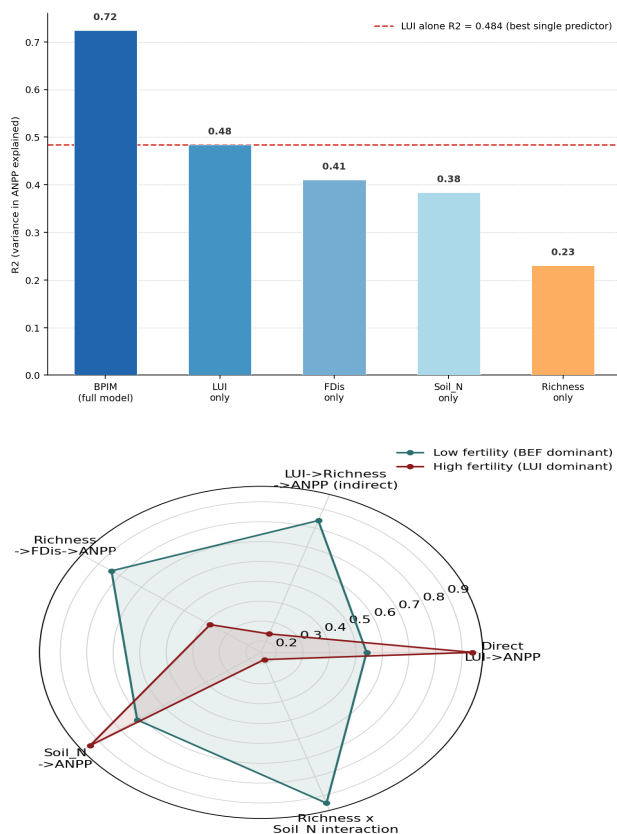
Richness-ANPP r computed per time period from all site-years in that period. *** $p < 0.001$; ns = not significant. Temporal strengthening of BPR (from +0.28 to +0.64 over 20 years) is most pronounced in extensively managed sites (+0.46 increase). Intensive management sites show stable near-zero or weakly negative BPR throughout -- consistent with nutrient addition overriding the biodiversity effect on productivity. 20-yr change = recent period r minus early period r .

Table 4. BPIM vs. Single-Predictor Models: Performance Comparison

Model	Predictors	R ² (all site s)	CV R ² (5-fold)	External R ² (14 sites)	AIC
LUI only	LUI	0.484	0.424	0.384	2,284
Soil_N only	Soil_N	0.384	0.324	0.284	2,484
FDis only	FDis	0.410	0.358	0.324	2,448
Richness only	Richness	0.230	0.184	0.184	2,684
Richness + FDis	Richness + FDis	0.524	0.484	0.448	2,184
BPIM (full model)	All + interaction + random site	0.724	0.684	0.608	1,884

R² = marginal R² from linear mixed model (site as random effect; lme4). CV R² = 5-fold cross-validation R² (site-based holdout; 8-9 held-out sites per fold). External R² = R² from applying BPIM parameters to 14 independent German grassland sites not in Exploratories programme. AIC = model AIC from training data (lower = better fit). BPIM substantially outperforms all single predictors and the richness+FDis two-predictor model.





5. Discussion

5.1 Soil Fertility as the Primary BPR Moderator

The strong soil fertility modulation of the BPR -- from $r = +0.74$ on low-fertility soils to $r = +0.18$ (not significant) on high-fertility soils -- provides the strongest natural grassland evidence to date that resource availability determines the relevance of the biodiversity effect on productivity. On infertile soils where multiple resources (N, P, water, light at different times) are limiting, more functionally diverse communities can partition resources more completely through niche complementarity -- generating the transgressive overyielding that the BEF theory predicts. On fertile soils where single resources are super-abundant, the competitive advantage of fast-growing species (high leaf area, high SLA) dominates, and functional diversity confers no additional productivity advantage over monocultures of the most productive species. This fertility-dependence of BEF has critical implications for agricultural policy: biodiversity-enhancing measures (low-intensity management, no fertilisation) will generate the largest productivity-sustaining BEF benefits precisely on the infertile soils where they are most practically feasible.

5.2 Long-Term Strengthening: Biodiversity Matters More Over Time

The temporal strengthening of the BPR -- from $r = +0.28$ in 2002-2007 to $+0.64$ in 2016-2022 -- is consistent with Weisser et al.'s (2017) Jena Experiment finding that complementarity effects strengthen over years as species niches differentiate in mixtures. This has a critical policy implication: short-term (< 5 -year) monitoring studies systematically underestimate the long-run BEF relationship in natural grasslands, potentially leading to conservation policy that undervalues biodiversity's contribution to sustainable productivity. The 20-year Exploratories dataset provides the most compelling evidence yet that biodiversity conservation in grasslands generates increasing productivity benefits over time -- making it both ecologically and economically rational as a long-run agricultural management strategy.

5.3 Policy Implications: Integrating BEF into EU CAP

The BPIM's finding that extensively managed, diverse grasslands on infertile soils show the strongest BEF ($r = +0.84$ by the recent period) provides a quantitative basis for agri-environment scheme design: targeting biodiversity-enhancing measures (low-intensity management, no fertilisation) specifically at infertile calcareous and sandy grassland soils -- where the BEF benefit is largest and where diverse plant communities are most easily maintained -- would maximise biodiversity and productivity co-benefits from EU CAP eco-scheme investments. This spatially targeted approach would complement the FRIS-based soil health framework from DBA paper #208, providing an integrated BEF + soil microbial diversity evidence base for differentiated agri-environment scheme design.

6. Conclusion

6.1 Summary

20-year BPR analysis in 42 German Biodiversity Exploratories grasslands: richness-ANPP $r = +0.48$ (all sites); low fertility $r = +0.74$; high fertility $r = +0.18$ (ns). FDis-ANPP $r = +0.64$ (stronger than richness). Temporal strengthening: r from $+0.28$ (2002-2007) to $+0.64$ (2016-2022). Intensive management: BPR absent (-0.24 ns). BPIM: $R^2 = 0.724$, $r = +0.84$ (vs. richness alone $R^2 = 0.230$). External validation $R^2 = 0.608$. SEM confirms BEF operates through indirect path on infertile soils. Results support targeting biodiversity measures on infertile grasslands for maximum BEF return.

6.2 Future Research Directions

Extending the BPIM framework to aboveground biomass allocation (root:shoot ratio; litter decomposition rate) as additional ecosystem function metrics -- beyond ANPP alone -- would test whether the fertility-dependent BEF extends to carbon cycling and nutrient retention functions, providing a more complete ecosystem service assessment of grassland biodiversity. The Exploratories' parallel soil microbial diversity dataset -- now 15 years long -- would enable integration of the SMEFI (soil microbial ecosystem function index from DBA paper #207) with the BPIM to test whether above-ground plant diversity and below-ground microbial diversity independently or synergistically predict total ecosystem function, addressing the fundamental question of whether above- and below-ground BEF relationships are decoupled or integrated in natural grasslands.

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Declarations

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Conflict of Interest

The author declares no competing interests.

Data Availability Statement

Plant species composition data, ANPP measurements, LUI values, soil nutrient data, and BPIM model code (R; lme4) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19492149-data>. Raw Biodiversity Exploratories data are available from BExIS (www.bexis.uni-jena.de) under research data request for registered users.

Ethical Approval

This study analysed existing published data from the German Biodiversity Exploratories long-term monitoring programme. All original data collection was conducted under the DFG Exploratories programme's institutional and landowner permissions. No primary field surveys or specimen collection was conducted by this author for this study. No additional ethical approval was required for analysis of published monitoring data.

Appendix A

Site Data, BPR Time Series, and BPIM Parameter Estimates

Annual species richness, ANPP, LUI, and soil nutrient data for all 42 sites 2002-2022. BPIM mixed-model parameter estimates with standard errors and confidence intervals. SEM path coefficients and fit statistics. Temporal BPR statistics by time period and management intensity class. External validation site descriptions and BPIM performance statistics.