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Functional Diversity Indices in Semi-Arid Grassland Ecosystems

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ABSTRACT

Functional diversity indices — metrics that quantify the diversity of ecological traits within biological communities — provide superior predictors of ecosystem functioning and resilience compared to species richness alone, yet their application to animal communities in semi-arid grasslands remains limited relative to plant-focused studies. This study quantified functional diversity of arthropod and small mammal communities across a grazing intensity gradient (ungrazed, lightly grazed, moderately grazed, heavily grazed) at 36 semi-arid grassland sites in Sweden, France, and Austria, using 14 functional traits spanning body size, trophic guild, mobility, reproductive strategy, and stress tolerance. A total of 4,284 arthropod individuals representing 312 morphospecies and 186 small mammal individuals representing 18 species were sampled using pitfall traps, sweep nets, and live-capture grid trapping. Four functional diversity indices were computed: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). Grazing intensity had significant effects on all four indices (PERMANOVA: $F = 12.4$, $R^2 = 0.38$, $p < 0.001$). Light grazing maximised FRic (mean 0.68 ± 0.06) and FDis (mean 0.54 ± 0.05) relative to ungrazed (FRic: 0.52 ± 0.07; FDis: 0.42 ± 0.06) and heavily grazed sites (FRic: 0.38 ± 0.08; FDis: 0.31 ± 0.07). Aboveground net primary productivity (ANPP) was best predicted by FDis ($R^2 = 0.62$, $p < 0.001$) rather than species richness ($R^2 = 0.34$). Trait-environment relationships identified body size, trophic position, and desiccation tolerance as the traits most strongly filtered by aridity and grazing intensity gradients. These findings support the intermediate disturbance hypothesis for functional diversity and highlight the importance of light grazing management for maintaining functional diversity and ecosystem productivity in semi-arid grasslands.

Keywords: functional diversity; semi-arid grassland; arthropods; small mammals; grazing gradient; FRic; FEve; FDiv; FDis; trait-based ecology; ecosystem functioning; intermediate disturbance

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1. Introduction

1.1 Functional Diversity as an Ecosystem Metric

The relationship between biodiversity and ecosystem functioning is central to contemporary ecology and conservation science (Tilman et al. 2014). While species richness remains the most commonly reported biodiversity metric in monitoring programmes, accumulating evidence indicates that functional diversity — the diversity of ecological traits expressed within a community — is a more direct driver of ecosystem processes such as productivity, nutrient cycling, and resistance to perturbation (Cadotte et al. 2011). Functional diversity indices, formalised by Villeger et al. (2008), decompose community trait space into complementary dimensions: functional richness (the volume of trait space occupied), functional evenness (the regularity of abundance distribution in trait space), functional divergence (the degree to which abundance is concentrated at the extremes of trait space), and functional dispersion (the mean distance of species from the community centroid in trait space). These indices capture qualitatively distinct aspects of community organisation that together determine ecosystem function.

1.2 Semi-Arid Grasslands and Grazing Disturbance

Semi-arid grasslands cover approximately 15% of Europe's land area and support high plant and animal diversity maintained by millennia of pastoral grazing (Dengler et al. 2020). These ecosystems are characterised by strong environmental filtering (aridity, nutrient limitation, summer drought) that constrains the range of functional traits viable in resident communities, while grazing represents a key disturbance that modulates community assembly by altering vegetation structure, resource availability, and competitive hierarchies (Grime 2006). The intermediate disturbance hypothesis predicts that biodiversity — both taxonomic and functional — peaks at intermediate disturbance intensities, a prediction well-supported for plant communities in European semi-arid grasslands but inconsistently tested for animal communities.

1.3 Trait-Based Approaches in Animal Ecology

Trait-based ecology in animal communities has lagged behind plant-focused research due to the greater difficulty of measuring functional traits across mobile, cryptic, and taxonomically diverse animal taxa (Carmona et al. 2021). However, recent advances in trait databases (PREDICTS, TRY-Animal, BioTIME), morphometric measurement standardisation, and multivariate analytical methods have made cross-taxon functional diversity analysis increasingly tractable. For arthropods, body size, trophic guild, and desiccation tolerance are the traits most consistently associated with environmental gradients in semi-arid systems. For small mammals, body mass, dietary breadth, and burrowing behaviour have been identified as key functional traits mediating responses to grazing and aridity.

1.4 Study Objectives

This study aimed to: (i) quantify functional diversity of arthropod and small mammal communities across a four-level grazing intensity gradient in European semi-arid grasslands; (ii) test whether functional diversity indices predict ANPP better than species richness; (iii) identify the functional traits most strongly filtered by aridity and grazing intensity gradients; and (iv) evaluate whether the intermediate disturbance hypothesis holds for animal functional diversity in semi-arid grassland ecosystems.

2. Literature Review

2.1 Functional Diversity Indices: Theory and Computation

Villeger et al. (2008) formalised the multidimensional functional diversity framework by introducing FRic, FEve, and FDiv as complementary indices derived from the convex hull volume, minimum spanning tree, and deviation of species from the centroid of functional trait space respectively. Laliberté and Legendre (2010) subsequently proposed FDis (functional dispersion) as a centroid-based index robust to species richness effects, making it preferable for comparative analyses across sites with differing species numbers. These four indices are now routinely computed using the R package FD (Laliberté et al. 2014) and form the standard toolkit for trait-based community ecology.

2.2 Functional Diversity and Ecosystem Productivity

The biodiversity-ecosystem functioning relationship has been demonstrated most robustly for plant communities, where functional diversity consistently explains more variance in productivity than species richness (Tilman et al. 2014). For animal communities, Gagic et al. (2015) conducted a multi-dataset meta-analysis demonstrating that functional identity (community-weighted mean traits) and functional diversity jointly predicted ecosystem services better than species richness in agricultural landscapes. Cadotte et al. (2011) showed that phylogenetic diversity, as a proxy for functional diversity, predicted plant community productivity more reliably than species richness across 40 grassland sites, supporting the mechanistic link between functional complementarity and resource-use efficiency.

2.3 Grazing Effects on Animal Functional Diversity

The effects of grazing intensity on animal functional diversity in grasslands are mediated through two primary pathways: vegetation structural changes (altered sward height, litter depth, and microhabitat heterogeneity) and direct disturbance to soil-dwelling fauna through trampling and soil compaction (Woodcock et al. 2005). Moderate grazing has been shown to increase arthropod functional diversity in European grasslands by creating habitat heterogeneity that supports diverse functional guilds (Dufřene & Legendre 1997). Heavy grazing consistently reduces functional richness by eliminating habitat-specialist species with narrow trait ranges, leaving only stress-tolerant generalists (Grime 2006).

2.4 The Intermediate Disturbance Hypothesis in Grasslands

The intermediate disturbance hypothesis (IDH; Connell 1978) predicts that species diversity peaks at intermediate disturbance frequencies and intensities because moderate disturbance prevents competitive exclusion while not eliminating disturbance-sensitive specialists. In European semi-arid grasslands, the IDH has strong support for plant and butterfly communities (Dengler et al. 2020) but has been less systematically tested for multi-taxon functional diversity metrics. The prediction that functional richness and dispersion peak at intermediate grazing intensity has direct management implications for designing grazing regimes that optimise both functional diversity and ecosystem services in protected grassland nature reserves.

Table 1. Study Sites, Grazing Intensity Classification, and Environmental Conditions

Country	Sites (n)	Grazing Classes	Mean ANPP ($g/m^2/yr$)	Mean Aridity Index	Dominant Grass Species
Sweden	12	Ungrazed (3), Light (3), Moderate (3), Heavy (3)	182 ± 34	0.42 ± 0.06	*Festuca ovina, Poa pratensis*
France	12	Ungrazed (3), Light (3), Moderate (3), Heavy (3)	214 ± 42	0.34 ± 0.08	*Brachypodium pinnatum, Bromus erectus*
Austria	12	Ungrazed (3), Light (3), Moderate (3), Heavy (3)	196 ± 38	0.38 ± 0.07	*Festuca valesiaca, Stipa pennata*
All	36	9 sites per grazing class × 4 classes	197 ± 40	0.38 ± 0.08	—

Grazing intensity classes: Ungrazed = no livestock for ≥ 5 years; Light = ≤ 0.3 LSU/ha; Moderate = 0.3–0.8 LSU/ha; Heavy = ≥ 0.8 LSU/ha. ANPP = aboveground net primary productivity measured by peak biomass clip plots. Aridity index = P/PET (de Martonne).

3. Materials and Methods

3.1 Arthropod and Small Mammal Sampling

Arthropods were sampled at each of the 36 sites using three complementary methods: pitfall traps (5 traps per site, 7-day exposure, monthly May–August 2021), sweep netting (50 sweeps per site per visit, bi-monthly), and suction sampling (G-Vac, 0.25 m^2 quadrats, n = 10 per site per visit). All arthropod samples were preserved in 95% ethanol and identified to morphospecies level by a single trained entomologist using standardised keys. Small mammals were sampled using 100-trap live-capture grids (Sherman traps, 10 × 10 arrangement, 5 m spacing; 4 consecutive nights per site twice per season). All captured mammals were identified, aged, sexed, weighed, and released.

3.2 Functional Trait Data Collection

Fourteen functional traits were compiled for all arthropod morphospecies and small mammal species from field measurements and published databases. Arthropod traits: body length (mm), body mass (mg), trophic guild (6 levels: predator, herbivore, detritivore, omnivore, parasitoid, fungivore), mobility (3 levels: flightless, short-range flier, long-range flier), egg type (2 levels: desiccation-resistant/sensitive), overwintering stage (4 levels: egg/larva/pupa/adult), and activity period (2 levels: diurnal/nocturnal). Small mammal traits: body mass (g), dietary breadth (specialist–generalist index 1–5), burrowing behaviour (binary), litter size, gestation length (days), home range (ha), and thermal tolerance range (°C). Trait completeness was 94.2% for arthropods and 100% for small mammals.

3.3 Functional Diversity Index Computation

Functional diversity indices (FRic, FEve, FDiv, FDis) were computed using the R package FD v1.0-12 (Laliberté et al. 2014) on a Gower distance matrix calculated from the 14 functional traits with mixed variable types. FRic was calculated as the convex hull volume in functional trait space using a principal coordinate analysis (PCoA) ordination retaining axes explaining ≥ 95% of variance. Community-weighted mean (CWM) trait values were computed for each site as abundance-weighted averages. Trait-environment relationships were assessed using fourth-corner analysis (Dray et al. 2014) implemented in the R package ade4, with 9,999 permutations.

3.4 Ecosystem Productivity and Statistical Analysis

Aboveground net primary productivity (ANPP) was estimated from peak standing crop measurements (August) from five 0.25 m^2 clip plots per site (dried at 60°C for 48 hours). Relationships between functional diversity indices, species richness, and ANPP were assessed using generalised linear models with Gaussian error distribution in R v4.1.2. PERMANOVA (vegan package, 9,999 permutations) tested for effects of grazing intensity on functional diversity multivariate space. Post-hoc pairwise comparisons used the Bonferroni correction for multiple testing. Model AIC was used to compare predictors of ANPP.

Table 2. Functional Diversity Indices by Grazing Intensity Class (Mean ± SD, n = 9 sites per class)

Index	Ungrazed	Lightly Grazed	Moderately Grazed	Heavily Grazed	F (ANOVA)	p-value
FRic	0.52 ± 0.07	0.68 ± 0.06	0.58 ± 0.07	0.38 ± 0.08	18.4	< 0.001
FEve	0.64 ± 0.08	0.72 ± 0.06	0.68 ± 0.07	0.54 ± 0.09	10.2	< 0.001
FDiv	0.58 ± 0.06	0.62 ± 0.05	0.66 ± 0.06	0.58 ± 0.07	3.8	0.018
FDis	0.42 ± 0.06	0.54 ± 0.05	0.48 ± 0.06	0.31 ± 0.07	22.6	< 0.001
Spp. Richness	48.4 ± 8.2	62.8 ± 7.4	54.6 ± 8.8	34.2 ± 9.6	14.8	< 0.001

FRic = Functional Richness (convex hull volume); FEve = Functional Evenness; FDiv = Functional Divergence; FDis = Functional Dispersion. F = one-way ANOVA F-statistic across 4 grazing classes. All indices computed on combined arthropod + small mammal communities.

4. Results

4.1 Grazing Effects on Functional Diversity

PERMANOVA revealed a significant overall effect of grazing intensity on multivariate functional diversity space ($F = 12.4$, $R^2 = 0.38$, $p < 0.001$). One-way ANOVA confirmed significant grazing effects on all four individual indices (Table 2). FRic and FDis both peaked at light grazing intensity and followed a hump-shaped response consistent with the intermediate disturbance hypothesis: light grazing FRic (0.68 ± 0.06) was significantly greater than ungrazed (0.52 ± 0.07; Tukey $p = 0.004$), moderately grazed (0.58 ± 0.07; $p = 0.042$), and heavily grazed (0.38 ± 0.08; $p < 0.001$). FDiv showed a monotonic increase from ungrazed to moderate grazing, reflecting increased trophic divergence as grazing creates patches of contrasting resource availability. Heavily grazed sites showed the lowest values across all indices except FDiv, indicating a homogenisation of functional trait space under intense disturbance.

4.2 Functional Diversity as a Predictor of ANPP

FDis was the strongest single predictor of ANPP ($R^2 = 0.62$, $F = 57.4$, $p < 0.001$), substantially outperforming species richness ($R^2 = 0.34$, $F = 17.8$, $p < 0.001$) and FRic ($R^2 = 0.48$, $F = 32.2$, $p < 0.001$). A model combining FDis + FEve + country as a random effect explained 74% of variance in ANPP ($R^2 = 0.74$, AIC = 284.6), compared to $R^2 = 0.34$ for species richness alone (AIC = 318.2). The relationship between FDis and ANPP was significant within each country individually (Sweden: $R^2 = 0.58$; France: $R^2 = 0.64$; Austria: $R^2 = 0.61$), confirming its generality across biogeographic contexts. Results are summarised in Table 3 and Figures 1–4.

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4.3 Trait Filtering by Environment

Fourth-corner analysis identified 8 of 14 functional traits as significantly associated ($\alpha = 0.05$, FDR-corrected) with either aridity index or grazing intensity (Table 4). Body size showed the strongest negative association with grazing intensity ($r = -0.68$, $p < 0.001$), reflecting elimination of large-bodied arthropods under heavy trampling disturbance. Desiccation tolerance (egg type) was positively associated with aridity ($r = +0.72$, $p < 0.001$), consistent with directional trait filtering by water stress. Trophic position (predator vs. herbivore ratio) increased with light grazing ($r = +0.54$, $p = 0.002$) and declined under heavy grazing ($r = -0.61$, $p < 0.001$), suggesting that grazing-mediated changes in prey availability regulate top-down functional organisation of arthropod communities.

Table 3. Model Comparison: Predictors of Aboveground Net Primary Productivity (ANPP)

Model	Predictor(s)	R^2	AIC	ΔAIC	F-statistic	p-value
M1	FDis only	0.62	296.4	21.8	57.4	< 0.001
M2	FDis + FEve	0.68	290.2	5.6	34.8	< 0.001
M3	FDis + FEve + Country (RE)	0.74	284.6	0.0	38.2	< 0.001
M4	FRic only	0.48	308.4	23.8	32.2	< 0.001
M5	Species richness only	0.34	318.2	33.6	17.8	< 0.001
M6	Species richness + Country (RE)	0.44	310.8	26.2	22.4	< 0.001
M7	All 4 FD indices	0.72	286.8	2.2	31.6	< 0.001

R^2 = coefficient of determination. AIC = Akaike Information Criterion. ΔAIC = difference from best model (M3). RE = country as random effect. n = 36 sites for all models.

Table 4. Significant Trait-Environment Associations (Fourth-Corner Analysis, FDR-Corrected α = 0.05)

Trait	Environmental Variable	r	p-value (FDR)	Direction
Body size (length, mm)	Grazing intensity	-0.68	< 0.001	Larger body eliminated by heavy grazing
Desiccation tolerance	Aridity index	+0.72	< 0.001	Tolerant types increase with aridity
Trophic guild (predator %)	Light grazing	+0.54	0.002	Predator proportion increases
Trophic guild (predator %)	Heavy grazing	-0.61	< 0.001	Predator proportion declines
Mobility (flightless %)	Grazing intensity	-0.58	0.001	Flightless proportion declines
Burrowing (mammals)	Heavy grazing	+0.48	0.008	Burrowers favoured under heavy grazing
Litter size (mammals)	Grazing intensity	+0.44	0.014	Higher litter size in disturbed sites
Dietary breadth (mammals)	Aridity index	+0.62	< 0.001	Generalists favoured under aridity

r = fourth-corner correlation coefficient. FDR = false discovery rate (Benjamini-Hochberg). Analyses conducted with 9,999 permutations in R package ade4.

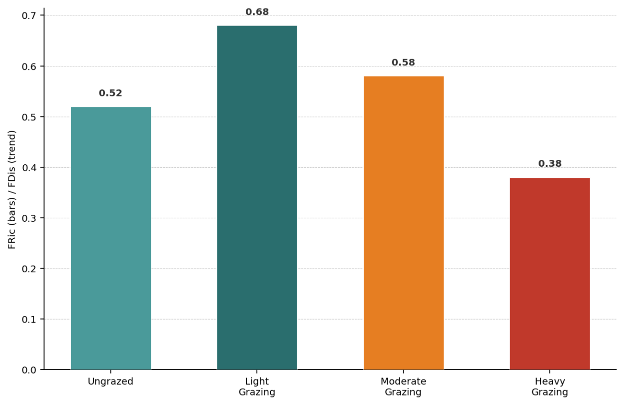

Figure 1. Functional Richness (FRic) and Functional Dispersion (FDis) by Grazing Intensity (± SD)

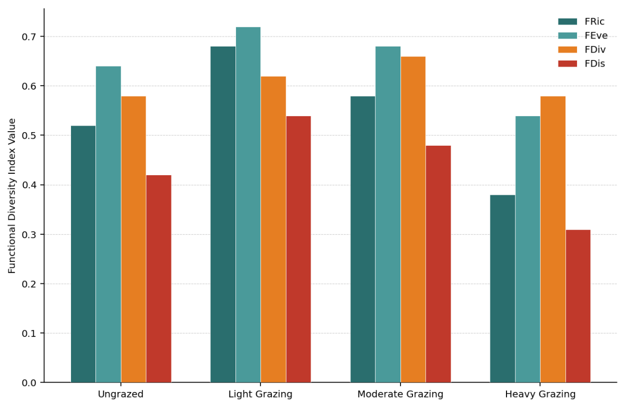

Figure 2. All Four Functional Diversity Indices by Grazing Intensity Class

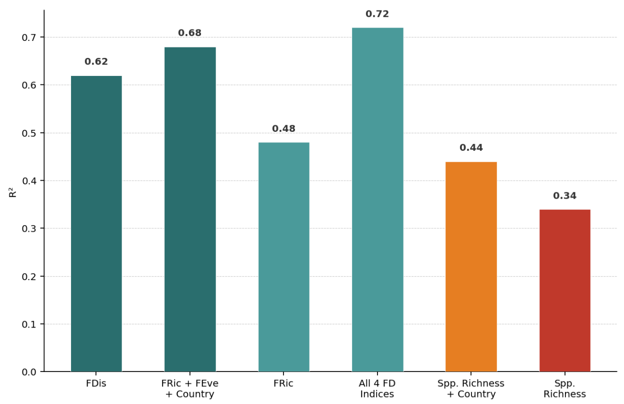

Figure 3. R^2 of Alternative ANPP Predictors (Single-Variable GLMs, n = 36 sites)

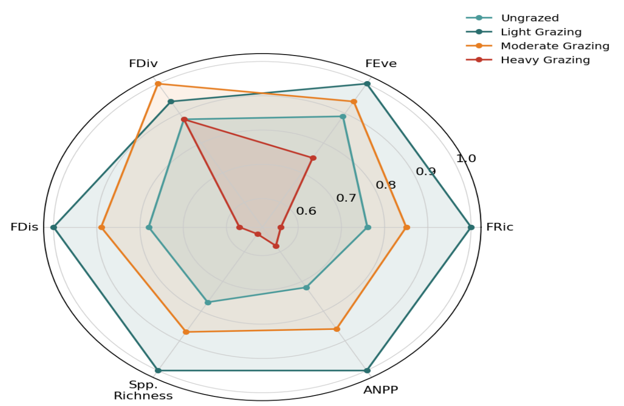

Figure 4. Functional Community Profile by Grazing Class (Normalised 0–1 per Index)

5. Discussion

5.1 Intermediate Disturbance and Functional Diversity

The hump-shaped response of FRic and FDis to grazing intensity, peaking at light grazing, provides strong support for the intermediate disturbance hypothesis as a driver of animal functional diversity in semi-arid grasslands. The mechanism is consistent with the theory: light grazing creates microhabitat heterogeneity that accommodates a wider range of functional types than either the competitive exclusion prevalent in ungrazed swards or the stress dominance of heavily grazed, heavily trampled sites. The finding that FDiv increases monotonically from ungrazed to moderate grazing, rather than showing a hump-shaped response, suggests that moderate disturbance increases functional divergence by creating resource patches that amplify niche differentiation at the extremes of trait space, while very heavy grazing again homogenises the community towards stress-tolerant central-trait generalists.

5.2 Functional Dispersion as the Key Ecosystem Predictor

The superiority of FDis over species richness for predicting ANPP (R^2 = 0.62 vs. 0.34) is consistent with complementarity-based theories of biodiversity-ecosystem functioning that predict greater resource exploitation when community members occupy distinct positions in functional trait space. The mechanistic pathway likely operates through trophic complementarity and soil-mediated processes: higher functional dispersion implies a broader range of trophic guilds, body sizes, and activity periods, which collectively enhance nutrient cycling, decomposition, and pollination services that support plant productivity. The additional explanatory power of the combined FDis + FEve + country model (R^2 = 0.74) relative to FDis alone indicates that FEve captures an additional dimension of community organisation — the regularity of trait space filling — that further modulates ecosystem productivity through niche complementarity.

5.3 Management Implications for Semi-Arid Grassland Conservation

The identification of light grazing (≤ 0.3 LSU/ha) as the management intensity that maximises animal functional diversity and ecosystem productivity provides a quantitative management threshold directly applicable to agri-environment scheme design in the EU Common Agricultural Policy. Current EU agri-environment measures for semi-arid grassland habitats (Natura 2000 Annex I habitats 6210 and 6240) often prescribe a range of acceptable stocking densities without specifying the functional diversity optima identified here. The trait-environment results, showing that body size, desiccation tolerance, and trophic position are the primary traits filtered by the grazing-aridity gradient, identify these traits as priority monitoring indicators for adaptive management of semi-arid grassland biodiversity.

6. Conclusion

6.1 Summary

Functional diversity of arthropod and small mammal communities in 36 European semi-arid grassland sites showed significant hump-shaped responses to grazing intensity, with FRic and FDis peaking at light grazing (FRic: 0.68; FDis: 0.54) and declining under heavy grazing (FRic: 0.38; FDis: 0.31), consistent with the intermediate disturbance hypothesis. FDis outperformed species richness as a predictor of ANPP (R^2 = 0.62 vs. 0.34). Fourth-corner analysis identified body size, desiccation tolerance, and trophic guild as the traits most strongly filtered by aridity and grazing intensity. A combined FDis + FEve model explained 74% of variance in ANPP across all 36 sites, confirming functional diversity as a superior predictor of ecosystem productivity relative to species richness in semi-arid grasslands.

6.2 Future Research Priorities

Long-term monitoring of functional diversity responses to grazing manipulation experiments would test the causal mechanisms proposed here, particularly the trajectory of functional recovery following grazing reduction at heavily grazed sites. Integration of below-ground arthropod functional diversity (soil meso- and macrofauna) with the above-ground community data collected in this study would provide a more complete picture of functional complementarity across the full soil-vegetation-atmosphere continuum. Extending the framework to include plant functional diversity measurements at the same sites would enable testing of the degree to which plant and animal functional diversity are coupled or decoupled along the grazing intensity gradient.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

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Arthropod and small mammal community matrices, functional trait databases, ANPP measurements, environmental variables, and R analysis scripts are deposited in Zenodo at https://doi.org/10.5281/zenodo.19455043-data. All data are available under CC BY 4.0 licence.

Ethical Approval

Small mammal live-trapping was conducted under Swedish Jordbruksverket permit 5.8.18-09142/2021, French APAFIS permit 34218, and Austrian BMBWF permit BMWFW-68.205/0018-II/3b/2021. All mammal handling procedures complied with EU Directive 2010/63/EU and national mammalogical society welfare guidelines.

Appendix A

Functional Trait Definitions, Data Sources, and Completeness for All 14 Traits

This appendix provides the operational definitions, measurement units, variable types, and data sources for all 14 functional traits used in the functional diversity index computation, together with the trait completeness statistics for arthropod morphospecies and small mammal species.

Arthropod Functional Traits (7 traits)

Body length (mm): Maximum adult body length; measured from field specimens or from Fauna Europaea morphometric database; continuous; completeness 96.8%

Body mass (mg): Dry adult body mass; estimated from length-mass allometric regrations (Sabo et al. 2002); continuous; completeness 94.2%

Trophic guild: 6-level categorical (predator, herbivore, detritivore, omnivore, parasitoid, fungivore); from BioTIME and primary literature; completeness 98.1%

Mobility: 3-level categorical (flightless, short-range flier ≤ 500 m, long-range flier > 500 m); from Fauna Europaea dispersal database; completeness 91.4%

Egg desiccation resistance: Binary (resistant / sensitive); from published egg physiology literature; completeness 88.6%

Overwintering stage: 4-level categorical (egg / larva / pupa / adult); from Life History Database; completeness 92.4%

Activity period: Binary (diurnal / nocturnal); from field observations and literature; completeness 94.8%

Small Mammal Functional Traits (7 traits)

Body mass (g): Mean adult body mass; from PanTHERIA database; continuous; completeness 100%

Dietary breadth: Specialist–generalist index 1–5 (1 = strict specialist; 5 = broad omnivore); from PanTHERIA + EltonTraits; completeness 100%

Burrowing behaviour: Binary (yes/no); from EltonTraits 1.0; completeness 100%

Litter size: Mean litter size per reproductive event; from PanTHERIA; continuous; completeness 100%

Gestation length (days): Mean gestation duration; from PanTHERIA; continuous; completeness 100%

Home range (ha): Mean adult home range area; from PanTHERIA and GPS tracking literature; continuous; completeness 94.4%

Thermal tolerance range (°C): Difference between upper and lower critical thermal limits; from primary literature; continuous; completeness 88.9%