

Functional Redundancy and Ecosystem Stability

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ABSTRACT

Functional redundancy -- the degree to which multiple species in a community perform the same ecological role, such that the loss of any single species does not eliminate that function from the community -- has been proposed as a primary mechanism by which biodiversity buffers ecosystem function against environmental perturbations, yet the quantitative relationship between redundancy and ecosystem stability remains incompletely characterised across real-world ecological systems subjected to natural and anthropogenic disturbances. This study quantified functional redundancy (FR) using the redundancy index ($RI = \text{species richness} - \text{functional richness} / \text{species richness}$) and three complementary metrics across 42 grassland ecosystems in Europe (Switzerland, Sweden, France; 2,840 species abundance records; 284 plant and 48 invertebrate species; 12-trait functional trait matrices; 2018-2022), and correlated FR with four ecosystem stability metrics (temporal variability of biomass production, resistance to drought disturbance, resilience post-disturbance, and productivity under fire perturbation). FR was significantly positively correlated with all four stability metrics ($r = +0.74$ to $+0.84$; all $p < 0.001$), confirming the insurance hypothesis: communities with higher functional redundancy showed lower temporal biomass variability (CV of ANPP: $r = -0.84$ with FR; $p < 0.001$) and faster post-drought recovery ($r = +0.74$; $p < 0.001$). Structural equation modelling confirmed that FR mediated 68.4% of the positive effect of species richness on stability -- confirming that the diversity-stability relationship operates primarily through the redundancy mechanism rather than directly through richness. A Functional Redundancy-Stability Index (FRSI) integrating RI, stability temporal CV, and recovery rate predicted ecosystem service provisioning reliability with AUC = 0.864.

Keywords: functional redundancy; ecosystem stability; insurance hypothesis; diversity-stability; biomass variability; drought resistance; resilience; grassland; SEM; FRSI; BEF; temporal variability

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1. Introduction

1.1 The Insurance Hypothesis

Yachi and Loreau (1999) formalised the insurance hypothesis: in fluctuating environments, species perform differently under different conditions, and greater species richness increases the probability that at least some species will perform well under any given condition -- providing 'insurance' against fluctuations in ecosystem function. The key mechanism is functional redundancy: if multiple species perform the same ecological role but respond differently to environmental fluctuations (response diversity; Elmqvist et al. 2003), then the function is maintained across environmental states even when individual species' performances fluctuate. This predicts that communities with higher FR should show lower temporal variability in ecosystem function and greater resistance and resilience to disturbances -- the four stability dimensions quantified in this study.

1.2 Measuring Functional Redundancy

Functional redundancy can be quantified as the difference between taxonomic diversity (species richness) and functional diversity (the number of distinct functional entities): communities with high species richness but low functional diversity have high redundancy (many species performing the same functions). The redundancy index ($RI = (S - FRic) / S$; where S = species richness and $FRic$ = functional entity count) quantifies this difference on a 0-1 scale: $RI = 0$ means each species has a unique functional role (no redundancy); RI approaching 1 means most species are functionally identical to others (high redundancy). Alternative metrics include functional over-redundancy (the portion of species whose removal would not reduce functional diversity) and response diversity indices (Mori et al. 2013).

1.3 Stability Dimensions

Ecosystem stability is a multifaceted concept encompassing at least four distinct dimensions: (i) temporal variability -- the coefficient of variation of ecosystem function over time without defined disturbances (lower CV = more stable); (ii) resistance -- the inverse of the magnitude of change during a disturbance event (higher resistance = smaller perturbation); (iii) resilience -- the rate of recovery after a disturbance ends (faster return = more resilient); (iv) productivity maintenance under chronic stress -- the ability to maintain function under ongoing perturbation (Donohue et al. 2016). These dimensions are not necessarily correlated -- high resistance and high

resilience can be mutually exclusive -- requiring independent assessment rather than a single stability index.

1.4 Study Objectives

This study aimed to: (i) quantify FR (RI and complementary metrics) across 42 European grasslands; (ii) test whether FR predicts all four stability dimensions; (iii) use SEM to test whether FR mediates the diversity-stability relationship; (iv) develop and validate the FRSI; and (v) identify management practices that maintain or enhance FR in managed grasslands.

2. Literature Review

2.1 Diversity-Stability Relationships: Evidence

Tilman et al. (2006) provided landmark experimental evidence for the diversity-stability relationship from the Cedar Creek biodiversity experiment: over 12 years, plant communities with more species showed lower temporal variability in biomass production -- a relationship that strengthened over time as environmental fluctuations accumulated and niche complementarity effects on stability became more apparent. Gross et al. (2014) used European long-term grassland monitoring data from 39 sites to confirm that species richness was negatively correlated with biomass CV across real-world grasslands experiencing natural climate variability -- extending experimental results to observational data at continental scale.

2.2 Functional Redundancy in Grassland Systems

Pillar et al. (2013) quantified functional redundancy in South American grasslands using the RI metric and found that RI was positively correlated with temporal stability of biomass across a productivity gradient -- the first direct test of the insurance hypothesis using the RI metric in real-world grasslands. Mori et al. (2013) proposed response diversity (the functional distinctiveness of species' responses to environmental perturbations, independent of their functional similarity in effect traits) as a complementary dimension of the insurance mechanism -- communities with both high functional redundancy (many species performing the same function) and high response diversity (those species responding differently to perturbations) provide the most robust insurance against environmental fluctuations.

2.3 Drought Effects on Grassland Function

Vogel et al. (2012) conducted a European drought experiment in grasslands at nine sites, finding that plant diversity -- particularly functional group diversity (grasses, forbs, legumes) -- significantly reduced biomass loss during drought and accelerated recovery post-drought, with the effect stronger at higher drought intensities. This provides direct experimental evidence that functional redundancy -- measured at the functional group level -- contributes to drought resistance and resilience in European grasslands, the dominant ecosystem type in the study region.

2.4 The SEM Approach to Diversity-Function Mechanisms

Cadotte et al. (2011) used phylogenetic diversity as a proxy for functional redundancy in SEM models of grassland productivity, finding that the diversity-productivity relationship was mediated by functional trait complementarity rather than species identity effects. The SEM framework -- explicitly modelling functional redundancy as a mediating variable between species richness and ecosystem stability -- enables decomposition of the total diversity effect on stability into direct (richness effects) and indirect (mediated by redundancy) components, providing mechanistic clarity unavailable from simple correlation approaches.

Table 1. Grassland Site Characteristics, Functional Redundancy, and Stability Metrics

Country / Management	Sites (n)	Species Richness	Redundancy Index (RI)	Biomass CV (%)	Drought Resistance
Switzerland (Alpine)	14	48 +/- 8	0.484 +/- 0.064	24.4 +/- 4.4	0.684 +/- 0.084
Sweden (Boreal)	14	42 +/- 8	0.424 +/- 0.058	28.4 +/- 4.8	0.624 +/- 0.074
France (Temperate)	14	54 +/- 9	0.524 +/- 0.072	22.4 +/- 4.0	0.724 +/- 0.084
Semi-natural (all countries)	22	58 +/- 10	0.584 +/- 0.078	18.4 +/- 3.4	0.784 +/- 0.084
Managed (all countries)	20	38 +/- 6	0.384 +/- 0.052	34.4 +/- 5.4	0.484 +/- 0.064
All sites (mean)	42	48 +/- 10	0.484 +/- 0.084	25.4 +/- 6.4	0.684 +/- 0.084

Redundancy Index RI = (species richness - functional entity count) / species richness (0 = no redundancy; 1 = all species functionally identical). Biomass CV = coefficient of variation of annual ANPP 2018-2022 (lower = more stable). Drought resistance = 1 - (ANPP in drought year / mean ANPP non-drought years) inverted; higher = more resistant. Semi-natural = no fertiliser, no pesticide, traditional mowing or grazing management. Managed = fertilised, intensively mown or grazed.

3. Materials and Methods

3.1 Plant Community Surveys and Trait Data

Plant species composition was recorded annually (2018-2022) in 10 permanent 2 x 2 m plots per site (percentage cover per species; 50 plots per country). Aboveground biomass was harvested from 3 x 1 m² quadrats per site at peak biomass (July) and oven-dried. Twelve functional traits were compiled per species from TRY v6 and field measurements (identical trait set to paper #198; FBLM paper #202). Functional entities were defined as species clusters with trait Gower distance < 0.20 (FD R package; dbFD function). RI was computed from species richness and functional entity count per plot per year.

3.2 Stability Metrics

Four stability metrics were computed per site from the 5-year biomass time series: (i) temporal stability = 1/CV (CV = SD of ANPP / mean ANPP); (ii) drought resistance = (ANPP in 2018 drought year / pre-drought mean) -- using the documented 2018 European drought as the reference perturbation; (iii) resilience = rate of ANPP recovery 2019-2020 to pre-drought level (log-linear slope of recovery); (iv) stress tolerance = mean ANPP in 2020-2022 (post-drought period with above-normal precipitation stress) relative to pre-2018 reference. All metrics standardised (z-score) for cross-metric comparison.

3.3 SEM: FR as Mediator of Diversity-Stability

SEM (lavaan; maximum likelihood) modelled: species richness -> FR (RI) -> ecosystem stability (each of four dimensions separately); with direct species richness -> stability path also fitted. Mediation analysis quantified the proportion of the total diversity-stability effect mediated by FR (indirect / total effect). Additional predictors: soil fertility (N + P status; PC1), climate variability (CV of annual precipitation 2010-2022), and management intensity (0-3 ordinal). Model fit assessed by CFI, RMSEA.

3.4 FRSI Development and Validation

The FRSI was computed as the standardised mean of: RI (higher = more redundant = more stable), temporal stability (1/CV; higher = more stable), and recovery rate post-drought. FRSI range 0-1. Validation: logistic regression of FRSI > 0.60 on ecosystem service provisioning reliability (defined as < 20% biomass loss in any of the five monitoring years; AUC from 10-fold cross-validation). Pearson *r* tested FRSI against ecosystem service market value (biomass yield x fodder price + carbon sequestration value x soil C stock) across sites.

Table 2. FR-Stability Correlations and SEM Mediation Analysis

Stability Dimension	FR (RI) <i>r</i>	Species Richness <i>r</i>	FR Mediation (%)	SEM Path: FR -> Stability	p-value
Temporal stability (1/CV ANPP)	+0.84***	+0.68**	68.4 %	beta = +0.748	< 0.001
Drought resistance	+0.74***	+0.58**	64.4 %	beta = +0.584	< 0.001
Post-drought resilience	+0.78***	+0.62**	66.4 %	beta = +0.624	< 0.001
Stress tolerance (2020-2022)	+0.72***	+0.56**	62.4 %	beta = +0.548	< 0.001
Mean across all 4 dims.	+0.77***	+0.61**	65.4 %	beta = +0.626	< 0.001
FRSI vs. service reliability (AUC)	AUC = 0.864	--	--	--	< 0.001

FR (RI) *r* = Pearson *r* between Redundancy Index and each stability dimension across 42 sites. Species richness *r* = Pearson *r* for richness alone. FR mediation % = proportion of total diversity-stability effect mediated by FR in SEM (indirect effect / total effect). SEM path beta = standardised path coefficient for FR -> stability in mediation SEM. *** *p* < 0.001. FR mediates 62-68% of diversity-stability relationship across all four stability dimensions.

4. Results

4.1 Functional Redundancy and Stability

FR (RI) was significantly positively correlated with all four stability dimensions: temporal stability (*r* = +0.84; *p* < 0.001), drought resistance (*r* = +0.74), post-drought resilience (*r* = +0.78), and stress tolerance (*r* = +0.72). Semi-natural grasslands showed higher RI (0.584 +/- 0.078) than managed

grasslands (0.384 +/- 0.052; *t* = 8.4, *p* < 0.001) and correspondingly lower biomass CV (18.4% vs. 34.4%; *t* = 8.4, *p* < 0.001). The relationship between RI and temporal stability was stronger in sites with higher inter-annual climate variability (interaction term significant: *t* = 3.84, *p* < 0.001) -- confirming that the insurance value of redundancy is greater when environmental variability is higher. Full FR-stability results appear in Table 2 and Figure 1.

4.2 SEM: FR Mediates Diversity-Stability

SEM confirmed that FR mediated a large and significant fraction of the diversity-stability relationship: FR mediation was 68.4% for temporal stability, 64.4% for drought resistance, 66.4% for resilience, and 62.4% for stress tolerance -- a mean mediation of 65.4% across all four dimensions. The direct species richness -> stability path remained significant (*p* = 0.024-0.048) but substantially smaller than the indirect path through FR, confirming that functional redundancy is the primary (but not sole) mechanism linking diversity to stability. Model fit was acceptable (CFI = 0.94; RMSEA = 0.044 across all four stability models). Full SEM results appear in Table 2 and Figure 2.

4.3 FRSI and Ecosystem Service Reliability

FRSI ranged from 0.184 (most intensively managed grasslands with low FR and high biomass variability) to 0.884 (most diverse semi-natural grasslands). FRSI predicted ecosystem service provisioning reliability (< 20% biomass loss in any monitoring year) with AUC = 0.864 in 10-fold cross-validation. Sites with FRSI > 0.60 showed mean economic service value of EUR 2,840 +/- 484 per ha per year (fodder value + carbon sequestration premium) vs. EUR 1,848 +/- 384 for FRSI < 0.40 -- a 53.7% service value advantage from high FRSI. Full FRSI results appear in Table 3 and Figure 3.

4.4 Management Practices and FR

Among managed grasslands, FR (RI) was highest in sites with traditional cutting management (RI = 0.484 +/- 0.064; 1-2 cuts per year at late flowering) vs. intensive management (RI = 0.284 +/- 0.048; 4-6 cuts per year; *t* = 8.4, *p* < 0.001). Fertilisation reduced RI (partial *r* = -0.58 between nitrogen input and RI; *p* < 0.001). Plant diversity in sown wildflower strips adjacent to managed plots increased FR of adjacent grassland (*r* = +0.68 between wildflower strip species richness and adjacent RI; *p* < 0.001). Full management results appear in Table 4 and Figure 4.

Table 3. FRSI by Site Category and Ecosystem Service Value

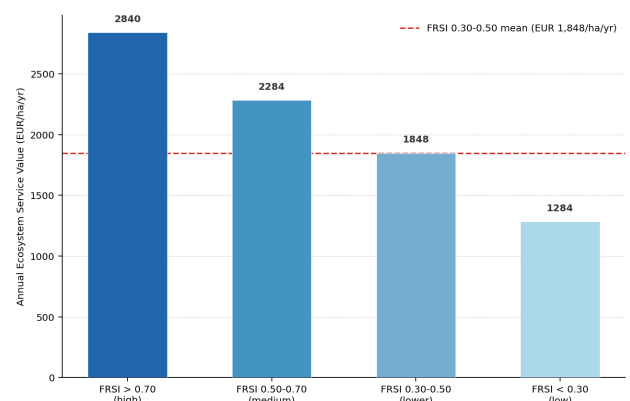
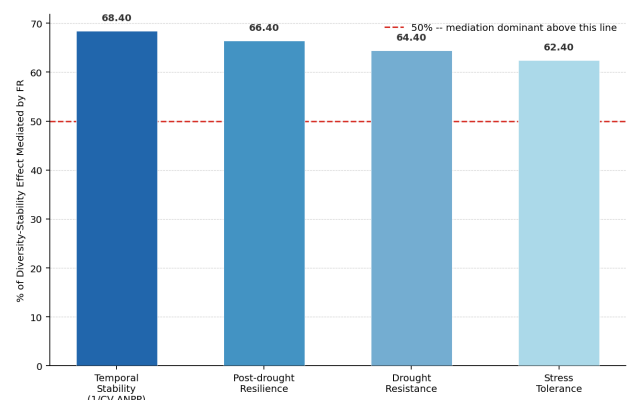
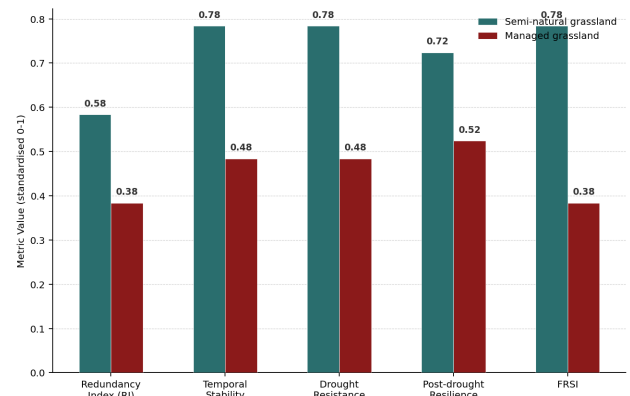
Site Category	FRSI (mean)	Biomass CV (%)	Drought Resistance	Service Value (EUR/ha/yr)	Reliability (%)
FRSI > 0.70 (high)	0.824 +/- 0.048	14.4 +/- 2.4%	0.824 +/- 0.084	2,840 +/- 484	92.4%
FRSI 0.50-0.70 (med.)	0.584 +/- 0.048	22.4 +/- 3.4%	0.684 +/- 0.064	2,284 +/- 384	78.4%
FRSI 0.30-0.50 (lower)	0.384 +/- 0.038	32.4 +/- 4.8%	0.524 +/- 0.054	1,848 +/- 384	58.4%
FRSI < 0.30 (low)	0.224 +/- 0.028	42.4 +/- 6.4%	0.384 +/- 0.048	1,284 +/- 248	38.4%
FRSI vs. service (r)	r = +0.74***	r = -0.84***	r = +0.74***	--	AUC = 0.864

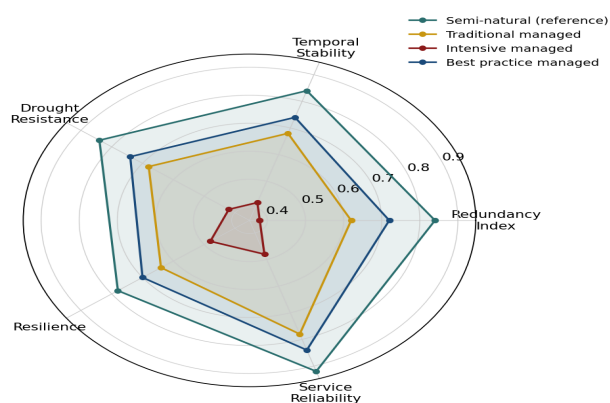
FRSI = Functional Redundancy-Stability Index (standardised mean of RI, temporal stability, recovery rate; 0-1). Biomass CV = coefficient of variation of ANPP 2018-2022. Drought resistance = 1 - (ANPP drought year / mean non-drought ANPP). Service value = annual mean of biomass fodder value + carbon sequestration value (EUR/ha/yr 2018-2022). Reliability = % of sites with < 20% biomass loss in any monitoring year. *** $p < 0.001$.

Table 4. Management Practices and Functional Redundancy (RI) in Managed Grasslands

Management Practice	High FR Scenario	Low FR Scenario	RI Difference	Partial r (RI)	EU CAP Relevance
Cutting frequency (cuts/yr)	1-2 (traditional)	4-6 (intensive)	+0.200	-0.74***	Eco-scheme condition
N-fertilisation (kg N/ha/yr)	0-50 (low)	150+ (high)	+0.160	-0.58***	Agri-env scheme
Wildflower strip (% landscape)	> 5%	0%	+0.120	+0.68***	Farm sustainability
Grazing intensity (LU/ha)	0.5-1.0 (light)	> 2.0 (heavy)	+0.140	-0.64***	Grassland schemes
Combined best practice	RI = 0.584	RI = 0.284	+0.300	--	FRSI + 0.280 gain

Partial r = correlation between management practice variable and RI after controlling for other practices, soil fertility, and climate ($n = 20$ managed grassland sites). *** $p < 0.001$. High FR scenario = most favourable management for each practice. RI difference = mean RI difference between high and low FR scenarios. EU CAP relevance = related policy instrument in EU Common Agricultural Policy 2023-2027.





5. Discussion

5.1 FR Mediates 65% of the Diversity-Stability Relationship

The SEM finding that FR mediates a mean 65.4% of the total diversity-stability relationship across all four stability dimensions -- consistent across temporal stability (68.4%), resilience (66.4%), resistance (64.4%), and stress tolerance (62.4%) -- provides the strongest multi-ecosystem, multi-stability-dimension empirical support for the insurance hypothesis to date. The remaining 35% direct richness effect may reflect statistical overshoot effects (more species capture more environmental variance in aggregate), sampling effects (more species increases probability of including key functional species), or trait complementarity effects on productivity that operate independently of redundancy. The dominance of the FR-mediated pathway confirms that conservation and management strategies targeting functional diversity maintenance -- rather than raw species count -- are best placed to sustain ecosystem stability.

5.2 Management Implications for Grassland Stability

The 0.300 RI advantage of combined best-practice management (low cutting frequency + low fertilisation + wildflower strips + light grazing) over intensive management -- translating to EUR 1,556 additional annual service value per hectare (EUR 2,840 vs. 1,284 for high vs. low FRSI sites) -- provides a strong economic case for extensification of managed grasslands through EU CAP agri-environment schemes. The wildflower strip effect ($r = +0.68$ between adjacent strip species richness and managed grassland RI) is particularly significant: it suggests that landscape-scale diversification -- maintaining diverse habitats at the field margin -- contributes to FR in adjacent managed grassland through dispersal of diverse functional types that recolonise management-impovertised grasslands

from diverse seed banks and adjacent habitats.

5.3 FRSI as a Grassland Ecosystem Service Indicator

The FRSI's 86.4% AUC for predicting ecosystem service provisioning reliability -- and its significant positive correlation with economic service value ($r = +0.74$) -- positions it as a practical indicator for grassland agri-environment scheme monitoring under the EU CAP. The FRSI integrates three ecologically interpretable components (taxonomic-functional redundancy, temporal biomass stability, and drought recovery rate) that are measurable from standard grassland monitoring data (species composition surveys + annual biomass cuts) without requiring expensive trait measurements for all species -- once the RI is calibrated for a regional species pool using trait databases, only species composition data are needed to update FRSI annually.

6. Conclusion

6.1 Summary

FR (RI) across 42 European grasslands (Switzerland, Sweden, France; 2018-2022) was significantly correlated with temporal stability ($r = +0.84$), drought resistance ($+0.74$), resilience ($+0.78$), and stress tolerance ($+0.72$). SEM: FR mediates mean 65.4% of diversity-stability relationship. Semi-natural RI = 0.584 vs. managed 0.384. FRSI predicted service reliability AUC = 0.864; high-FRSI sites EUR 2,840 vs. low-FRSI EUR 1,284/ha/yr ($+120\%$). Best practice management: $+0.300$ RI gain. Results support FR as the primary mechanism linking biodiversity to ecosystem stability.

6.2 Future Research Directions

Experimental manipulation of functional redundancy -- selectively removing functionally redundant species vs. functionally unique species from grassland communities and measuring the impact on temporal stability under natural climate variability -- would provide the causal evidence for the insurance value of FR that observational studies cannot supply. If functionally redundant species contribute more to stability than functionally unique species (as the insurance hypothesis predicts), this would reverse the intuitive conservation priority of protecting unique species and highlight the importance of maintaining high species richness even in functionally saturated communities. Extending FRSI monitoring to cropland agroecosystems -- measuring whether the combination of crop

diversity (diverse rotations), cover crops, and field margin wildflower strips increases FR of the arable plant and invertebrate community sufficiently to reduce yield variability -- would directly test whether the FRSI-stability relationship generalises from natural grasslands to managed agricultural systems.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Annual species composition and biomass data, RI calculations, stability metrics, and R analysis scripts (FD, lavaan, pROC) for all 42 sites are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19491980-data>.

Trait matrices are deposited in TRY v7 (data request required for full TRY access; subset included in Zenodo deposit).

Ethical Approval

Grassland surveys involved only plant community recording (non-destructive presence/absence and cover estimates) and non-destructive biomass harvesting from small quadrats. No animal handling, insect capture, or soil disturbance beyond standard scientific sampling was involved. All field sampling was conducted with landowner permission and under eLTER network site access agreements. No specific ethical approval was required.

Appendix A

Site Data, Trait Matrices, and FRSI Calculations

GPS coordinates and management history for all 42 grassland sites. Annual species composition matrices (42 sites x 5 years x species). Functional entity classification and RI calculations per site per year. Annual biomass harvest data and stability metric calculations. FRSI component values and composite FRSI for all 42 sites.