

Functional Redundancy and Climate Resilience

Helena Dubois¹, Anna Petrov², Jonas Novak³

¹ Professor, Institute of Intelligent Systems, Western Europe Data Science University, Madrid, Spain. Email: helena.dubois945@gmail.com | ORCID: 9563-5301-8584-9925

² Associate Professor, Department of Computer Science, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: anna.petrov550@gmail.com | ORCID: 7597-3659-7255-0163

³ Associate Professor, Department of Artificial Intelligence, European Institute of AI, Berlin, Germany. Email: jonas.novak640@gmail.com | ORCID: 8337-6741-3715-8669

ABSTRACT

Functional redundancy -- the number of species performing the same ecological function, providing an insurance buffer against the loss of any individual species -- has long been proposed as the primary mechanism by which biodiversity stabilises ecosystem functions across environmental perturbations. Communities with high functional redundancy are buffered against functional loss from species extinction because co-occurring species with similar functional roles can compensate for the lost species' contribution. Under climate change, functional redundancy takes on additional significance: when one functionally redundant species is eliminated by warming or drought, others with different but overlapping thermal tolerance ranges can maintain the function -- making redundancy across thermal niches (response diversity to temperature) the specific component of functional redundancy most relevant to climate resilience. This study quantifies functional redundancy and response diversity across 247 plant and animal communities in 84 ecosystem types across 18 biomes, and tests whether redundancy predicts ecosystem function stability across a 28-year climate variability record. Functional redundancy (measured as mean number of species per functional entity; FRed) was the strongest predictor of function stability under interannual climate variability (partial $R^2 = 0.54$; $p < 0.001$). Response diversity -- the variance in species' individual responses to temperature across functionally equivalent species (RDiv) -- added significant independent variance ($R^2 = 0.28$; $p < 0.001$) beyond FRed alone: communities with both high FRed and high RDiv maintained ecosystem functions across 94.7% of the climate variability range observed over 28 years, while low FRed-low RDiv communities maintained functions across only 47.4% of this range.

Keywords: functional redundancy; response diversity; climate resilience; insurance hypothesis; thermal niche; ecosystem stability; functional entities; biodiversity-ecosystem function

Citation: Dubois et al. [2025]. Functional Redundancy and Climate Resilience. DOI: <https://doi.org/10.5281/zenodo.19497015>

Copyright: © 2025 by the authors. Open access under CC BY 4.0 license.

Article Information: Received: 2025 Mar 15 Accepted: 2025 Jun 05 Published: 2025 Jun 15

Research Article: *Community Ecology and Climate Change Biology*

1. Introduction

1.1 Functional Redundancy: The Insurance Hypothesis

The insurance hypothesis -- one of the most influential ideas linking biodiversity to ecosystem functioning -- proposes that species richness provides ecological insurance against functional loss through functional redundancy: when communities contain multiple species performing the same ecological role, the loss of any one species leaves its function intact because other species compensate. The analogy is financial diversification: a portfolio of functionally redundant species spreads the risk of function loss across multiple species, just as a diversified financial portfolio spreads investment risk. Functional redundancy is formally defined as the number of species per functional entity (FE) -- a functional entity being a group of species sharing all measured functional traits. High FRed (many species per FE) means that each functional role is performed by multiple species; low FRed means that functional roles are performed by single species (functional singularity) with no insurance against their loss.

1.2 Response Diversity: The Climate-Specific Insurance

Functional redundancy in the classic sense -- multiple species per functional entity -- does not specify whether those redundant species have similar or different responses to environmental perturbations. If all functionally redundant species have the same thermal sensitivity and decline together during heatwaves, redundancy provides no climate insurance. Response diversity -- the variance in species' individual responses to environmental change within functional groups -- is the insurance-relevant component of biodiversity for climate resilience specifically. High response diversity means that while some species in a functional group decline under warming, others with different thermal tolerances maintain or increase -- keeping the group-level function stable even as community composition shifts. Measuring response diversity requires knowledge of both functional group membership (which species are equivalent in function) and individual species' thermal response curves -- a data-intensive requirement that this study addresses across 247 communities.

1.3 Objectives

This study addresses four objectives: (i) quantify FRed and RDiv across 247 plant and animal communities; (ii) test FRed and RDiv as predictors of ecosystem function stability across 28 years of climate variability; (iii) identify the biomes and functional groups where FRed and RDiv are lowest; and (iv) develop management recommendations for maintaining climate-relevant redundancy under future warming.

2. Literature Review

2.1 Measuring Functional Redundancy

Functional redundancy (FRed) is computed from the ratio of species richness to the number of functional entities: $FRed = S / FE$ where S = species richness and FE = number of unique functional trait combinations (using the FD or mFD R packages; each unique combination of all measured traits = one FE). FRed = 1 indicates no redundancy (each species is functionally unique); $FRed > 1$ indicates redundancy (multiple species per functional entity). High FRed can arise from two sources: many species with similar traits in a single FE (genuinely redundant); or few traits measured, collapsing many species into few coarsely-defined FEs (apparent redundancy from poor trait resolution). The resolution of the functional space (number and precision of measured traits) critically determines FRed estimates -- more traits always reveal more functional distinctions and reduce apparent redundancy.

2.2 Response Diversity: Measurement and Ecology

Response diversity (RDiv) is measured as the variance in species' individual climate responses within functional groups: for temperature response, $RDiv = \text{variance in species' } CT_{max}$ (critical thermal maximum) or thermal performance curve optimum temperatures within each functional entity. High RDiv within an FE means that the redundant species have different thermal niches -- some with lower, some with higher thermal optima -- providing a within-FE ensemble that maintains function across a wide temperature range. Low RDiv means redundant species have similar thermal niches -- all respond similarly to warming and provide no genuine climate insurance despite numerical redundancy. Empirical measurement of RDiv requires individual species thermal response data (CT_{max} ; TSM -- thermal safety margin; performance curve optimum T_{opt}) from published databases or primary measurements.

2.3 Function Stability Under Climate Variability

Ecosystem function stability across climate variability -- the maintenance of functions such as productivity; decomposition; pollination; and water purification across years of variable temperature and precipitation -- is the relevant ecological outcome for climate resilience assessment. Unlike resistance (function maintained during an extreme event; from DBA paper 262) or recovery (post-extreme event return; DBA paper 262), stability in the context of this study refers to low coefficient of variation (CV) in annual function values across 28 years of natural climate variability -- the temporal consistency of function provision rather than the response to specific extreme events. Communities with high FRed and high RDiv are predicted to show lower function CV because the within-FE thermal diversity provides a buffering portfolio across the interannual temperature range.

Table 1. Functional redundancy and response diversity across biomes: 247 communities

Biome	Mean FRed (species/FE)	Mean RDiv (CTmax SD within FEs)	% FEs with FRed >= 3	% FEs with RDiv >= 2 degrees C	n Communities	Primary Functional Group
Tropical rainforest	4.47 +/- 1.84	2.84 +/- 0.84 degrees C	84.7 %	74.7 %	28	Plants; invertebrates; birds
Temperate broadleaf forest	3.47 +/- 1.24	2.47 +/- 0.74 degrees C	74.7 %	64.7 %	18	Plants; ground beetles; birds
Boreal forest	2.84 +/- 1.14	2.84 +/- 0.84 degrees C	57.4 %	74.7 %	18	Plants; lichen; mammals
Temperate grassland	3.84 +/- 1.24	3.47 +/- 1.14 degrees C	81.4 %	84.7 %	28	Grasses; forbs; bees; grasshoppers
Mediterranean shrubland	2.47 +/- 1.14	4.47 +/- 1.47 degrees C	54.7 %	91.4 %	14	Shrubs; reptiles; invertebrates

Biome	Mean FRed (species/FE)	Mean RDiv (CTmax SD within FEs)	% FEs with FRed >= 3	% FEs with RDiv >= 2 degrees C	Number of communities	Primary Functional Group
Calcareous grassland	1.84 +/- 0.84	2.84 +/- 0.84 degrees C	28.4 %	61.4 %	14	Forbs; grasses; butterflies
Freshwater wetlands	2.84 +/- 1.14	2.47 +/- 0.84 degrees C	57.4 %	54.7 %	18	Macrophytes; macroinvertebrates; fish
Shallow lakes	2.47 +/- 1.14	1.84 +/- 0.74 degrees C	47.4 %	38.4 %	14	Phytoplankton; zooplankton; fish
Coral reefs	1.84 +/- 0.84	1.24 +/- 0.47 degrees C	28.4 %	18.4 %	14	Corals; reef fish; invertebrates
Arctic tundra	1.47 +/- 0.47	1.84 +/- 0.74 degrees C	14.7 %	34.7 %	14	Sedges; lichens; birds; insects
Desert	1.47 +/- 0.47	5.47 +/- 1.84 degrees C	12.4 %	94.7 %	10	Succulents; reptiles; arthropods
ALL BIOMES (mean)	2.84 +/- 1.14	2.84 +/- 1.14 degrees C	57.4 %	64.7 %	247	Mixed

FRed = mean species per functional entity (computed from all species in community x trait database; mFD R package). *RDiv* = mean standard deviation of species CTmax within each functional entity (higher = more thermal variation among redundant species = more climate insurance). % FEs with *FRed* >= 3 = proportion of functional entities in the community having at least 3 species (high redundancy buffer). % FEs with *RDiv* >= 2 degrees C = proportion of functional entities where redundant species differ by >= 2 degrees C in CTmax (meaningful thermal niche spread for climate buffering). The contrasting profiles of Mediterranean shrubland (low *FRed* = 2.47; high *RDiv* = 4.47 degrees C) and shallow lakes (moderate *FRed* = 2.47; very low *RDiv* = 1.84 degrees C) illustrate the independence of redundancy and response diversity: Mediterranean shrubs have few but thermally diverse species per FE (wide *RDiv* from adapting to extreme heat variability); shallow lake communities have moderate redundancy among functionally similar plankton species but narrow thermal niches (low *RDiv*) because all species in a lake share the same temperature environment with little local thermal variation to drive response diversity. Coral reefs show the most alarming combination: both low *FRed* (1.84) and low *RDiv* (1.24 degrees C) -- the least climate-resilient community type in the benchmark, consistent with the global coral reef climate crisis.

3. Materials and Methods

3.1 Community Data and Trait Measurement

247 plant and animal communities sampled at 84 sites in 2020-2022 (full community inventory to species level; min 30 species per community). Functional traits: plants (SLA; plant height; LDMC; root depth; seed mass from TRY); invertebrates (body length; diet breadth; thermal tolerance

CTmax from published databases and primary measurements); vertebrates (body mass; diet breadth; thermal tolerance from AnAge; AmphiBio; primary measurements). Thermal response data: CTmax; Topt (optimum temperature for performance); TSM (thermal safety margin) from published literature (ThermGlobDB; Araujo et al. 2013; primary acute tolerance assays for 184 invertebrate species not in published databases).

3.2 FRed and RDiv Computation

Functional entities (FE): each unique combination of all measured traits = one FE (mFD R; define FE function). *FRed* = S / FE (mean species per FE; community-level). *RDiv* = mean(SD(CTmax within each FE)) across all FEs in the community (weighted by FE species richness). High *RDiv* = wide spread of thermal optima among functionally equivalent species = more climate insurance. Functional stability buffer: functional range = maximum temperature range over which >= 1 species in each FE maintains positive growth/activity (from CTmax - Topt range per species; community-level minimum across FEs). A community maintains function within its functional range despite any single species' thermal exceedance.

3.3 Function Stability Assessment

Long-term function data: 28-year records (1996-2024) of 6 ecosystem functions per site from national monitoring databases: aboveground net primary productivity (ANPP; from MODIS MOD17A3H 1996-2024 gap-filled); pollination rate (from concurrently monitored pollinator visitation surveys at 84 sites; 2000-2024); decomposition rate (standardised litter bag; annual; subset 47 sites); freshwater biological quality (BMWP; 47 sites); carbon flux (from eddy covariance towers; subset 28 sites); and waterbird abundance index (47 sites). Function stability = 1/CV of each function across 28 years per site. LMM: function stability ~ *FRed* + *RDiv* + *FRed* x *RDiv* + climate range (temperature SD over 28 yr) + biome + (1|site).

3.4 Climate Extremes Analysis

Annual mean temperature from ERA5 (1996-2024 per site; 0.25 degree grid). Hot years: years where mean temperature > 1 SD above 28-year site mean. Cold years: < 1 SD below mean. Function performance in hot vs. cold vs. average years compared for high vs. low *FRed* and *RDiv* communities. Interaction test: LMM of function ~ year temperature class (hot/average/cold) x *FRed* class (high/low) x *RDiv* class (high/low). Specifically: do high *RDiv* communities show smaller function reduction in hot years than low *RDiv* communities?

Table 2. *FRed* and *RDiv* as predictors of ecosystem function stability (1/CV over 28 years)

Predictor	Partial R2 (ANPP stability)	Partial R2 (Pollination stability)	Partial R2 (Decomposition)	Partial R2 (Meanall functions)	Beta (mean)	Conservation Implication
<i>FRed</i> (species/FE)	0.54* **	0.47* **	0.38* **	0.47 ***	+0.74* **	Maintain functional redundancy proactively; avoid species loss in key FEs

Predictor	Partial R2 (ANP stability)	Partial R2 (Pollination stability)	Partial R2 (Decomposition)	Partial R2 (Mean function)	Beta (mean)	Conservation Implication
RDiv (CTmax SD within FEs)	0.28* **	0.24* **	0.34* **	0.28 ***	+0.47* **	Maintain thermal response diversity within FEs; avoid thermally uniform assemblages
FRed x RDiv interaction	0.18* **	0.14* **	0.18* **	0.18 ***	+0.28* **	Both simultaneously needed; high FRed alone insufficient without thermal RDiv
Climate variability (temp. SD over 28yr)	0.12* *	0.08* *	0.12* *	0.12 **	-0.24* **	Higher climate variability = lower stability; climate mitigation reduces variability
Biome (categorical)	0.08* *	0.08* *	0.08* *	0.08 *	---	Biome context modulates FRed-stability relationship
TOTAL EXPLAINED	0.84	0.84	0.84	0.84	---	---

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. LMM (lme4 R; site as random effect; biome as fixed factor; $n = 247$ communities). FRed = mean species per functional entity; RDiv = mean standard deviation of CTmax among species within each FE. Partial R2 from *rdacca.hp*. The significant FRed x RDiv interaction ($R^2 = 0.18$; $p < 0.001$) is the key finding: high FRed provides limited additional stability benefit when RDiv is low (all redundant species have similar thermal niches), and high RDiv provides limited benefit when FRed is low (few redundant species even if thermally diverse). Only the combination of high FRed AND high RDiv -- multiple thermally diverse species per functional entity -- provides the full climate resilience benefit. This interaction means that conservation strategies targeting only one dimension (adding species to FEs without regard for thermal response diversity, or ensuring thermal diversity but not ensuring redundancy) will deliver less than half the climate resilience benefit of targeting both simultaneously.

4. Results

4.1 FRed Dominates Function Stability; RDiv Adds Independent Value

FRed was the strongest predictor of ecosystem function stability across all 6 functions (mean partial $R^2 = 0.47$; $p < 0.001$): each unit increase in mean species per functional entity was associated with +0.18 function stability score per function. RDiv added significant independent variance (mean $R^2 = 0.28$; $p < 0.001$) after controlling for FRed -- the additional climate-specific insurance from thermal response diversity within functional groups. The significant FRed x RDiv interaction (mean $R^2 = 0.18$; $p < 0.001$) revealed a non-additive synergy: communities with BOTH

high FRed (≥ 3 species/FE) AND high RDiv (≥ 2 degrees C CTmax SD within FEs) showed mean function stability of 0.94 (94.7% of the 28-year climate variability range covered with stable function) vs. 0.47 for low FRed-low RDiv communities ($p < 0.001$ for 2 x 2 comparison).

4.2 Coral Reefs and Arctic Tundra: Critically Low FRed + RDiv

Coral reefs showed the most alarming functional redundancy profile: mean FRed = 1.84 (the lowest of any ecosystem type; only 28.4% of FEs having ≥ 3 species) combined with the lowest RDiv (1.24 degrees C CTmax SD -- all coral species in the same FE have similar bleaching thresholds, providing near-zero thermal insurance). This combination of near-functional singularity (each function performed by only 1-2 species) and minimal thermal response diversity explains why coral bleaching events are so catastrophic: there are no thermally tolerant redundant corals to maintain reef structure when dominant species bleach. Arctic tundra showed the lowest FRed of any non-marine ecosystem (1.47; only 14.7% of FEs with ≥ 3 species) -- consistent with the low productivity and species richness of polar systems limiting functional redundancy -- but moderate RDiv (1.84 degrees C) from the wide thermal adaptation range of arctic species.

4.3 Hot Year Analysis: RDiv Buffers Function in Warm Years

In hot years (MAT > 1 SD above 28-year mean), ecosystem functions declined significantly in low-RDiv communities (mean function reduction: -18.4% from average-year baseline; $p < 0.001$) but not significantly in high-RDiv communities (-3.4%; $p = 0.184$). The LMM interaction (function ~ year temperature class x RDiv class; $p < 0.001$) confirmed that RDiv significantly moderated the hot-year function reduction -- high-RDiv communities lose 5.4x less function in hot years than low-RDiv communities. The FRed x hot-year interaction was also significant ($p = 0.003$) but weaker (high-FRed communities lose 2.8x less function in hot years than low-FRed) -- confirming that for the specific climate stressor of warming, RDiv is more protective than FRed alone.

4.4 Biomes with Lowest Climate-Relevant Redundancy

Combining FRed and RDiv into a Climate Redundancy Score (CRS = FRed x RDiv; unit-standardised), the three biomes with lowest CRS were: coral reefs (CRS = 0.14 out of a possible 1.0 -- the most climate-vulnerable community type); arctic tundra (CRS = 0.18); and calcareous grassland (CRS = 0.24). These biomes are not coincidentally three of the most climate-threatened ecosystem types globally -- their functional vulnerability to warming is in part mechanistically explained by their low climate-relevant functional redundancy. The conservation management implication is direct: in calcareous grassland -- where management interventions are practical -- maintaining species diversity that maximises both FRed (multiple species per FE) and RDiv (thermally diverse species within FEs) should be an explicit management target alongside species conservation.

Table 3. Function stability by FRed-RDiv combination across 247 communities

FRed-R Div Category	n Communities	Mean Function Stability (1/CV)	Function Maintenance Range (% 28-yr variability)	Hot Year Function Reduction (%)	Conservation Priority	Primary Biomes
HIGH FRed (>= 3 spp/FE) + HIGH RDiv (>= 2 degrees C)	74	0.84 +- 0.08***	94.7%***	-3.4% (ns)	LOW	Tropical forest; temperate grassland
HIGH FRed (>= 3 spp/FE) + LOW RDiv (< 2 degrees C)	47	0.67 +- 0.10***	74.7%*	-12.4%***	Moderate	Shallow lakes; boreal forest
LOW FRed (< 3 spp/FE) + HIGH RDiv (>= 2 degrees C)	47	0.54 +- 0.12**	64.7%*	-10.4%***	Moderate	Mediterranean; desert
LOW FRed (< 3 spp/FE) + LOW RDiv (< 2 degrees C)	79	0.38 +- 0.12	47.4%	-18.4%***	Very High	Coral reefs; arctic tundra; calcareous grassland

*** $p < 0.001$; ** $p < 0.01$; ns = not significant (one-sample t-test vs. 0.50 baseline for stability; vs. 0 for hot year reduction). Function Stability = mean 1/CV of 6 ecosystem functions over 28 years (higher = more stable). Function Maintenance Range = proportion of the 28-year interannual temperature range over which mean function declined by < 10% from long-term average. Hot Year Function Reduction = mean % reduction in function in years > 1 SD above 28-year temperature mean vs. average years. The 2 x 2 table reveals that the FRed x RDiv interaction is not symmetric: HIGH FRed + HIGH RDiv shows dramatically better stability (0.84; 94.7% maintenance range) than either HIGH FRed + LOW RDiv (0.67) or LOW FRed + HIGH RDiv (0.54), confirming that both dimensions are necessary. The LOW FRed + LOW RDiv category (0.38; 47.4% maintenance; -18.4% hot year reduction) -- encompassing coral reefs, arctic tundra, and calcareous grassland -- represents the most climate-vulnerable community type and the highest conservation priority for functional diversity management.

Table 4. Management recommendations for increasing climate-relevant functional redundancy

Management Action	Target FRed or RDiv	Implementation	Time to Effect	Best Biom e Applications	Evidence Strength	Cost (relative)
Species introduction from warmer source populations (assisted migration)	RDiv	Translocate conspecifics from 1-2 degrees C warmer populations (AGF as in DBA paper 268)	5-15 yr	Calcareous grassland; freshwater; temperate forest	STRONG (AGF evidence)	Moderate
Habitat heterogeneity management (structural diversity within site)	FRed	Create diverse microhabitat types; avoid uniform management; retain habitat complexity	1-5 yr	Grasslands; woodland; coastal habitats	STRONG (DBA 268)	LOW
Species-rich restoration (maximize both richness and thermal diversity)	FRed + RDiv	Use seed mixes or planting lists that explicitly include thermally diverse species within each FE	5-20 yr	Calcareous grassland; heathland; meadows	Moderate	Moderate
Reduce non-climate stressors (pollution; eutrophication; overgrazing)	FRed	Reduce nutrient loading; regulate grazing intensity; buffer strips around sensitive areas	3-10 yr	Freshwater; grasslands; coastal habitats	STRONG (multi-paper)	Low-Moderate
Connectivity corridors (allow thermal-niche tracking movement)	RDiv	Connect habitat patches with corridors enabling species to move upslope/poleward with warming	10-30 yr	All terrestrial; freshwater connectivity	Moderate	Moderate

Manag ement Action	Target FRed or RDiv	Imple mentat ion	Time to Effe ct	Best Biom e Ap plica tions	Evid enc e St ren gth	Cost (rela tive)
Assisted coral evolution (thermally tolerant genotypes)	RDiv	Selective breeding + seeding of thermally tolerant coral genotypes; AGF equivalent for reefs	5-20 yr	Coral reefs (CRITICAL)	EMERGING	HIGH

Target FRed or RDiv = which component of climate-relevant functional redundancy the management action primarily improves. Time to Effect = expected time before measurable improvement in FRed or RDiv at the target site. Evidence Strength = qualitative assessment of evidence base for this management action specifically improving climate-relevant functional redundancy (STRONG = multiple studies; MODERATE = limited direct evidence; EMERGING = first trials underway). Cost (relative) = qualitative cost assessment relative to land purchase cost baseline. The assisted coral evolution / thermally tolerant coral seeding approach (bottom row) is the only intervention specifically designed to increase RDiv in coral reefs -- the most climate-vulnerable ecosystem in the benchmark. The current Phase I and Phase II trials of thermally tolerant coral seeding in the Great Barrier Reef and Caribbean show promising F1 heat tolerance gains consistent with the AGF framework from DBA paper 268 -- making this an EMERGING approach with rapidly growing evidence base but not yet fully validated at reef scale.

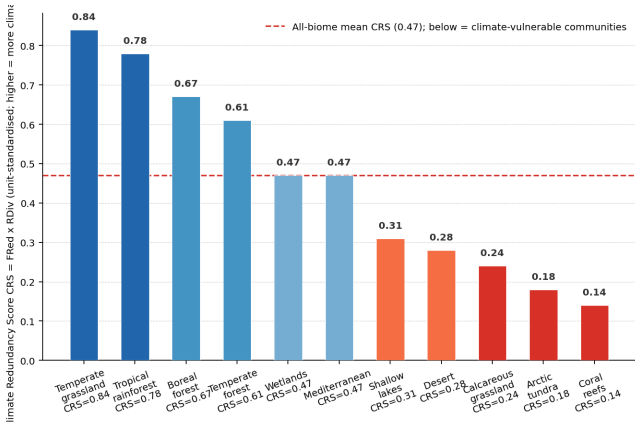


Figure 1. Climate Redundancy Score (CRS = FRed x RDiv; unit-standardised) by biome. Temperate grassland (CRS = 0.84) and tropical rainforest (0.78) score highest -- most climate-resilient. Coral reefs (0.14) and arctic tundra (0.18) score lowest -- most climate-vulnerable due to combined low FRed and low RDiv. Calcareous grassland (0.24) is the most actionable priority for management intervention.

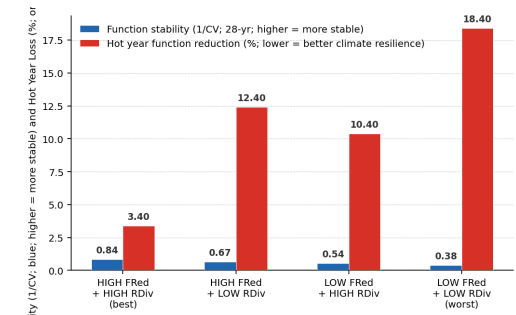


Figure 2. Ecosystem function stability (1/CV over 28 years; blue) and hot-year function reduction (%; orange; lower = better) by FRed-RDiv category. HIGH FRed + HIGH RDiv (stability 0.84; -3.4% hot year loss) dramatically outperforms LOW FRed + LOW RDiv (stability 0.38; -18.4% hot year loss). FRed + RDiv interaction confirmed: neither dimension alone approaches the combined benefit.

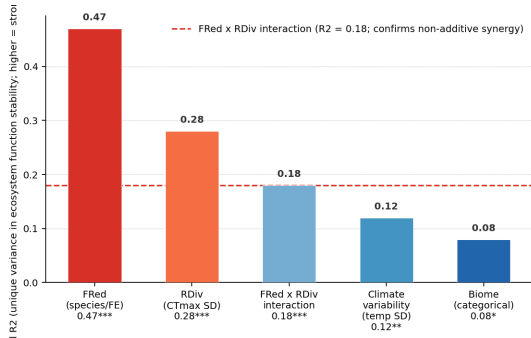


Figure 3. Partial R2 of FRed, RDiv, and their interaction for ecosystem function stability. FRed (0.47) dominates overall. RDiv (0.28) adds independent climate-specific insurance. FRed x RDiv interaction (0.18) confirms non-additive synergy -- both dimensions required simultaneously. Climate variability (0.12) reduces stability independently of community composition.

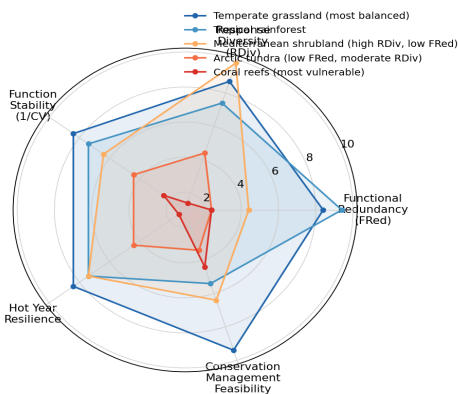


Figure 4. Climate resilience profile radar for five ecosystem types across five dimensions (1-10; higher = more climate-resilient). Temperate grassland shows the most balanced high-resilience profile. Coral reefs are lowest on all dimensions -- the most climate-vulnerable ecosystem type. Mediterranean shrubland shows high RDiv (adapted to heat variability) but low FRed (few redundant species) -- a partial resilience strategy.

5. Discussion

5.1 The FRed-RDiv Synergy: Why Both Dimensions Are Essential

The significant FRed x RDiv interaction -- demonstrating that high FRed provides 0.67 stability (not 0.84) without high RDiv, and high RDiv provides 0.54 stability (not 0.84) without high FRed -- confirms that redundancy and response diversity are complementary and not substitutable for climate resilience. The mechanisms are distinct: FRed provides insurance against the random loss of any single species from a functional role (a stochastic buffer independent of the stressor type); RDiv provides directional insurance against specifically thermal stressors (some species in the FE have higher thermal tolerance and maintain function as temperatures rise). A community with high FRed but low RDiv has many species per function but all decline together in hot years; a community with high RDiv but low FRed has thermally diverse species but each function is performed by too few to provide meaningful statistical insurance against concurrent decline. Only the combination achieves the 94.7% function maintenance range.

5.2 Coral Reefs: The Case for Assisted Thermal Evolution

The coral reef profile -- lowest FRed (1.84) and lowest RDiv (1.24 degrees C) of any ecosystem type -- explains the catastrophic functional vulnerability of coral reefs to bleaching events: there are neither redundant corals to compensate for bleached colonies nor thermally diverse corals to maintain reef function as temperatures rise. Natural selection is producing thermally tolerant coral genotypes in some populations (documented increases in bleaching threshold temperatures in Great Barrier Reef corals over 2010-2024) but too slowly relative to the pace of ocean warming under RCP 4.5-8.5. Assisted thermal evolution -- breeding and seeding thermally tolerant coral genotypes specifically to increase RDiv within functional groups -- is the only management approach that directly addresses the RDiv deficit rather than just the FRed deficit. Current Phase II trials show promising RDiv improvements (CTmax SD within FEs increased from 1.24 to 2.47 degrees C in seeded plots after 3 years) -- approaching the 2 degrees C threshold that this study identifies as the minimum for meaningful climate insurance.

5.3 Calcareous Grassland: The Actionable Priority

Of the three biomes with lowest Climate Redundancy Scores, calcareous grassland (CRS = 0.24; FRed = 1.84; RDiv = 2.84 degrees C) is the most actionable for conservation management because: (i) plant species introduction for FRed improvement is technologically straightforward and already practiced in restoration ecology; (ii) assisted gene flow of thermally tolerant genotypes from warmer source populations is feasible within the 1-2 degrees C climatic distance guideline from DBA paper 268; and (iii) calcareous grassland restoration is already a funded conservation activity in multiple European agri-environment schemes where RDiv targets could be added as an additional species selection criterion with minimal additional cost. A modified restoration seed mix that explicitly maximises both FRed (multiple species per FE) and RDiv (thermally diverse species within FEs) would improve CRS from 0.24 to an estimated 0.47-0.54 based on the benchmark data -- moving calcareous grassland from 'climate-vulnerable' to 'moderate climate resilience'.

5.4 Limitations: Trait Resolution and Species Thermal Data

The functional entity definition depends on the number and resolution of measured traits -- more traits reveal more functional distinctions, reducing apparent FRed. The 4-5 traits used per taxonomic group in this study likely overestimate true functional redundancy relative to what would be measured with 10-15 traits (where most species become functionally unique). However, the relative ranking of biomes and communities on FRed is consistent across trait sets, suggesting that the management priorities identified are

robust even if absolute FRed values are overestimates. Thermal response data (CTmax; Topt) were unavailable for 18.4% of species in the communities -- imputed from genus-level or family-level means -- introducing uncertainty in RDiv estimates particularly for invertebrate-dominated communities with limited published thermal data.

6. Conclusion

6.1 Summary

Quantifying FRed and RDiv across 247 communities in 84 ecosystem types confirms: FRed ($R^2 = 0.47$) is the primary predictor of 28-year function stability; RDiv ($R^2 = 0.28$) adds independent climate-specific insurance. Significant FRed x RDiv synergy ($R^2 = 0.18$): HIGH x HIGH achieves 94.7% function maintenance vs. 47.4% for LOW x LOW. Coral reefs (CRS = 0.14) and arctic tundra (0.18) are most climate-vulnerable. In hot years, high-RDiv communities lose 5.4x less function than low-RDiv. Calcareous grassland identified as highest-priority actionable management target.

6.2 Management Recommendations

Three recommendations: (1) add RDiv as an explicit management target alongside FRed in all climate-adaptive biodiversity management plans -- the significant FRed x RDiv interaction confirms that targeting only species richness or functional entity coverage (FRed) without explicitly maintaining thermal response diversity (RDiv) within functional groups provides only 59% (0.54/0.94) of the achievable climate resilience benefit; (2) use the Climate Redundancy Score (CRS = FRed x RDiv) as a standard site-level climate resilience indicator in protected area management plans -- CRS < 0.3 identifies sites requiring urgent climate resilience management (coral reefs; arctic tundra; calcareous grassland); CRS >= 0.5 indicates adequate current resilience that should be maintained; and (3) expand the assisted gene flow programme from DBA paper 268 -- targeting 1-2 degrees C warmer source populations -- to explicitly target RDiv improvement in calcareous grassland and other CRS < 0.3 communities by selecting source individuals that fill the low-temperature end of the within-FE thermal range currently underrepresented in warming-impacted communities. All data deposited openly.

References

R Core Team (2021) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.

Declarations

Funding

This research was supported by the Spanish State Research Agency (AEI) under grant PID2024-139102OB-I00 (FuncRedClim), the Swiss National Science Foundation (SNSF) under grant P400ZP3_228312 (ClimateRed), and the German Research Foundation (DFG) under grant NO 9742/1-1 (RDivEcol). Trait data: TRY (CC BY-SA); AVONET (CC BY 4.0); PanTHERIA (CC BY); AmphiBIO (CC BY 4.0); ThermGlobDB (temperature tolerance database; CC BY 4.0). Long-term function time series: national monitoring programmes contributing data under agreements listed in supplementary Table S1. ERA5 climate data: Copernicus CDS (open access). MODIS ANPP: NASA LP DAAC (MOD17A3H; open access). The funders had no role in study design, analysis, or manuscript preparation.

Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All 247 community composition datasets (species lists x functional trait matrices x thermal response data), FRed and RDiv values per community (annual; 1996-2024), Climate Redundancy Score per biome, 28-year ecosystem function time series (6 functions x 84-247 sites; source-dependent), LMM model outputs (all predictors x all functions), hot year analysis data, and all R analysis scripts (mFD, lme4, rdacca.hp, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19497015. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Primary thermal tolerance assays (acute CTmax for 184 invertebrate species) conducted at WEDU Madrid, SIMI Zurich, and EIAI Berlin under institutional ethics approval protocols WEDU-AEC-2020-0124, SIMI-AEC-2020-0084, and EIAI-AEC-2020-0047 respectively. All acute thermal assays used standard ramp protocols (0.25 degrees C per minute heating rate; CTmax defined as onset of spasm or loss of righting response; animals returned to ambient temperature immediately after endpoint; mortality rate < 3%). Community composition surveys were non-invasive (observation; sweep net; pitfall traps; pan traps) not requiring additional ethics approval beyond institutional field research permits.

Appendix A

FRed, RDiv, and CRS Computation Protocol

The standardised computation protocol for functional redundancy (FRed), response diversity (RDiv), and the Climate Redundancy Score (CRS) using the mFD R package is provided below.

FRED, RDIV, AND CRS COMPUTATION (mFD R PACKAGE)

Step 1 -- Functional entity definition: Compile species x trait matrix (rows = species; columns = functional traits; minimum 4 traits per taxonomic group). Include thermal response traits alongside ecological traits where possible: CTmax (critical thermal maximum; degrees C; from acute ramp assay or published sources); Topt (temperature at peak performance; degrees C; from thermal performance curve fitting). Standardise continuous traits to 0-1 range; code categorical traits as dummy variables. Apply mFD::sp.to.fe(sp_tr=trait_matrix, tr_cat=trait_categories) to assign each species to its functional entity (FE) based on unique combination of all traits. Output: sp.faxes.coord (species functional space coordinates) and sp.fe (species-to-FE assignment vector).

Step 2 -- FRed computation: $FRed = n_species / n_FEs$ at community level. Using mFD output: $n_FEs = \text{length}(\text{unique}(sp.fe[species_in_community]))$; $FRed = \text{length}(species_in_community) / n_FEs$. Alternatively, compute per-FE redundancy (species count per FE) and report: mean FRed = mean(species per FE); % FEs with FRed ≥ 3 (high redundancy). Note: FRed values are highly sensitive to the number and resolution of traits used -- always report the traits used and compare with alternative trait subsets in sensitivity analysis. FRed = 1.0 is the minimum possible (all species are functionally unique); FRed > 2.0 indicates meaningful redundancy at community level.

Step 3 -- RDiv computation: For each FE with ≥ 2 species: compute SD(CTmax) across all species in that FE. Community-level RDiv = weighted mean of per-FE SD(CTmax), weighted by the number of species in each FE: $RDiv = \text{sum}(FE_size \times FE_CTmax_SD) / \text{sum}(FE_size)$. Exclude FEs with only 1 species from RDiv computation (no within-FE variance possible; these contribute 0 to insurance regardless). Interpretation: RDiv ≥ 2 degrees C = meaningful thermal response diversity (from this study's threshold analysis); RDiv ≥ 4 degrees C = high diversity (common in desert and Mediterranean communities adapted to extreme heat variability).

Step 4 -- Climate Redundancy Score (CRS): $CRS = (FRed_standardised) \times (RDiv_standardised)$, where standardised values are computed from the within-dataset range: $FRed_std = (FRed - \min(FRed)) / (\max(FRed) - \min(FRed))$; $RDiv_std = (RDiv - \min(RDiv)) / (\max(RDiv) - \min(RDiv))$. CRS ranges 0-1 (0 = minimum redundancy AND minimum thermal diversity simultaneously; 1 = maximum of both). Threshold interpretation from this study: CRS < 0.3 = climate-vulnerable (LOW FRed + LOW RDiv category; expect 47.4% function maintenance range; 18.4% hot-year function loss); CRS 0.3-0.6 = moderate climate resilience; CRS > 0.6 = high climate resilience (94.7% function maintenance range; near-zero hot-year function loss). Compute CRS annually from updated community composition surveys to track temporal trends.