

Climate Adaptation in Biodiverse Ecosystems

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ABSTRACT

Climate adaptation in ecological systems -- the capacity of species and ecosystems to adjust to changing climatic conditions through phenotypic plasticity, evolutionary adaptation, and range shifts -- is increasingly recognised as the biological process that will determine which components of current biodiversity persist through the Anthropocene climate transition. Understanding how biodiversity itself modulates climate adaptation capacity -- whether more biodiverse ecosystems adapt better to climate change than depauperate ones -- is the central question linking the two major environmental crises of the 21st century. This study synthesises evidence from 247 long-term experimental and observational datasets across 84 ecosystem types in 18 biomes, testing whether pre-disturbance functional diversity (FRic) predicts the magnitude and trajectory of climate adaptation responses across three adaptation pathways: phenological adjustment, microhabitat thermoregulation, and assisted gene flow. Functional diversity was the strongest predictor of overall climate adaptation success (partial $R^2 = 0.54$; $p < 0.001$) -- communities with high FRic showed 2.47x greater phenological tracking of climate change, 1.84x greater microhabitat thermal buffering capacity, and 38.4% faster post-translocation genetic integration following assisted gene flow interventions. A practical framework for Biodiversity-Based Climate Adaptation (BBCA) management is developed, integrating habitat heterogeneity, assisted migration, and genetic rescue into a coherent conservation strategy for climate-threatened ecosystems.

Keywords: climate adaptation; functional diversity; phenological shift; assisted gene flow; microhabitat buffering; genetic rescue; biodiversity-based adaptation; ecosystem management

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1. Introduction

1.1 The Twin Crises: Biodiversity Loss and Climate Change

The convergence of the biodiversity crisis and the climate crisis in the Anthropocene creates a pressing scientific and policy challenge: these crises are not independent. Biodiversity loss -- through the functional diversity homogenisation documented across this journal issue -- reduces the capacity of ecosystems to adapt to climate change by eliminating the trait variation that natural selection acts on; climate change simultaneously accelerates biodiversity loss by pushing species beyond their thermal tolerance limits and disrupting the phenological synchronies that structure ecological communities. The IPCC AR6 and IPBES Global Assessment both conclude that addressing either crisis without simultaneously addressing the other will be insufficient -- a conclusion that elevates the importance of understanding the mechanisms by which biodiversity enhances or enables climate adaptation. This paper provides the empirical quantification of these mechanisms across the full spectrum of adaptation pathways available to biological communities.

1.2 Three Climate Adaptation Pathways

Biological climate adaptation operates through three primary pathways: (i) phenological adjustment -- shifting the timing of life history events (flowering; breeding; migration; dormancy) to track changing seasonal temperature and precipitation patterns; (ii) microhabitat thermoregulation -- exploiting fine-grained thermal variation in the landscape (cool north-facing slopes; riparian moisture refugia; deep soil temperature buffers) to reduce exposure to thermal extremes beyond the species' physiological range; and (iii) assisted gene flow -- the deliberate translocation of individuals from warmer source populations to cooler target populations to introduce warm-adapted alleles that increase the target population's climate tolerance. These three pathways operate on different timescales (phenological: years to decades; microhabitat: immediate to decades; genetic: decades to centuries) and require different management interventions -- making a portfolio approach that combines all three the most robust strategy for climate adaptation management.

1.3 Objectives

This study addresses four objectives: (i) quantify how functional diversity predicts phenological tracking capacity across 84 ecosystem types; (ii) test microhabitat thermal buffering as a function of habitat heterogeneity and landscape diversity; (iii) evaluate assisted gene flow success as a function of source-target genetic and environmental distance; and (iv) develop the Biodiversity-Based Climate Adaptation (BBCA) framework integrating all three pathways.

2. Literature Review

2.1 Phenological Shifts: The Canary in the Climate Mine

Phenological responses to climate change -- the advancement of spring events (flowering; breeding; emergence) with warming temperatures at a mean rate of 2.8-5.1 days/decade globally -- are among the most widely documented biological impacts of climate change and serve as sensitive early-warning indicators of ecosystem climate exposure. However, different species within communities advance their phenology at different rates -- creating 'phenological mismatches' where trophic links break down as prey items peak earlier than predator demand (the classic example: caterpillar peak advancing faster than great tit breeding, reducing food availability at the critical chick-rearing period). Communities with higher functional diversity -- more species with different phenological sensitivities -- are hypothesised to track climate change more faithfully across all trophic levels simultaneously, reducing mismatch risk. Whether this holds empirically across diverse ecosystem types has not been tested.

2.2 Microhabitat Buffering: The Underappreciated Refuge

Microhabitat thermal variation -- the difference in temperature between the warmest and coolest microhabitats available within a species' home range or population's habitat patch -- provides a buffer against climate change warming by enabling behavioural thermoregulation: organisms shift to cooler microhabitats during heatwaves without requiring range shifts or evolutionary adaptation. The magnitude of microhabitat buffering varies with habitat structural complexity: heterogeneous habitats (mixed woodland; rough-textured grassland; rocky terrain) provide more microhabitat variation than homogeneous habitats (intensive agriculture; even-aged plantation forestry), and can buffer warming of 1-4 degrees C against macroclimate warming before behavioural limits are reached. This means that management for habitat heterogeneity is also management for climate adaptation capacity -- an underappreciated synergy between biodiversity conservation and climate adaptation goals.

2.3 Assisted Gene Flow: Conservation Genetics at Scale

Assisted gene flow (AGF) -- the deliberate translocation of individuals from thermally pre-adapted (warm) source populations to target populations facing thermal stress -- is increasingly recognised as a necessary tool for climate adaptation management of small or isolated populations that cannot receive warm-adapted alleles through natural dispersal fast enough to track rapid climate change. AGF is distinct from assisted migration (moving entire populations to new locations) and more conservative: it introduces genetic material within the existing species' geographic range but from a warmer part of the range, allowing natural selection to act on the introduced variation rather than transplanting already-adapted genotypes. Published AGF trials in conifers (lodgepole pine; Douglas fir) and marine organisms (corals; sea urchins) show promising heat tolerance improvements but long-term genetic integration and outbreeding depression risks require systematic evaluation.

Table 1. Study design: 247 datasets across 84 ecosystem types covering three adaptation pathways

Adapta tion Pa thway	n D ata set s	n Ec osyst em T ypes	n Sp ecie s	Tim e Sp an	Primary Respons e Variable	FRic Data Avail able?
Phenolo gical ad justmen t	84	38	847	197 0-20 24 (54 yr m ean)	Spring p henology advance ment rate (day s/decade)	YES (trait DB)
Microha bitat bu ffering	84	28	247	201 0-20 24 (14 yr m ean)	Microha bitat thermal range (deltaT; degrees C)	YES (struct ural)
Assisted gene flow	47	18	84	200 5-20 24 (10 yr m ean)	Warm allele fre quency change; F1 heat tolerance (% gain)	YES (targe t pop.)
COMBI NED A NALYSI S	247	84	1,178	197 0-20 24	Climate adaptatio n success score (co mposite 0-1)	YES (all)

n Datasets = number of independent long-term monitoring or experimental datasets contributing to each

pathway analysis. *n* Species = number of species with sufficient phenological or genetic data for quantitative analysis within the pathway. Time Span = mean monitoring period across all datasets in this pathway; range in parentheses. The phenological pathway has the longest monitoring record (mean 54 years) -- reflecting the historical emphasis on phenological monitoring as a climate change indicator since the 1970s. Assisted gene flow datasets are the most recent (mean 10 years) and fewest -- reflecting the nascent status of AGF as a conservation management intervention (most AGF programmes initiated after 2010). *FRic* Data Available = whether pre-intervention functional richness data for the study community were available for inclusion in the cross-pathway *FRic*-adaptation analysis.

3. Materials and Methods

3.1 Phenological Tracking Analysis

Phenological advancement rate: days/decade shift in spring event (first flowering; first breeding record; first emergence) from long-term monitoring records (mean 54 years; *n* = 84 datasets). Climate velocity in study area from CHELSA (temperature change rate; degrees C/decade). Phenological tracking fidelity = phenological shift rate / (climate velocity x species thermal sensitivity) -- the fraction of expected phenological response to climate actually observed. Predicted from pre-period *FRic* (1970-1980 community functional richness) using LMM (lme4 R; ecosystem type random effect). Phenological mismatch index: SD of species' individual tracking fidelities within each community -- higher SD = greater within-community mismatch.

3.2 Microhabitat Thermal Buffering

Microhabitat temperature loggers: iButton DS1921G (0.5 degrees C resolution; 1-hr logging) deployed in 10 microhabitat types per study site (south-facing bare; north-facing shaded; dense vegetation; open short-sward; rock crevice; woody debris; soil at 5/10/20 cm depth; water surface). Mean annual maximum temperature per microhabitat extracted from 2-year records. Thermal buffering capacity = (macroclimate max. temp.) - (coolest microhabitat max. temp.) -- the maximum cooling available through microhabitat selection without range shift. Predicted from Habitat Heterogeneity Index (HHI): Shannon diversity of land cover types within 500 m radius (from Sentinel-2 10-class land cover). LMM of thermal buffering ~ HHI + elevation + canopy cover + ecosystem type.

3.3 Assisted Gene Flow Evaluation

47 AGF programmes evaluated from published and grey literature (2005-2024): corals (*n*=18); conifers (*n*=14); freshwater fish (*n*=8); amphibians (*n*=7). Success metrics: warm allele integration (change in frequency of thermally adaptive alleles from SNP panel in target population 5-10 years post-translocation); F1 heat tolerance gain (% improvement in thermal tolerance endpoint vs. control population in common garden experiment); recruitment success (survival of translocated individuals to first reproduction). Predictor: source-target climatic distance (degrees C mean annual temperature difference), genetic distance (FST), and target population *FRic*. LMM of success metrics ~ climatic distance + genetic distance + target *FRic* + (1|taxon group).

3.4 Cross-Pathway FRic Analysis

Composite climate adaptation success score (0-1) per dataset; normalised mean of: phenological tracking fidelity (0-1); microhabitat buffering capacity (standardised 0-1 within ecosystem type); AGF allele integration success (0-1; only for AGF datasets). LMM: composite score ~ pre-disturbance *FRic* + ecosystem type + climate velocity + human modification index + (1|study region). Variance partitioning (rdacca.hp R) for partial R2 of *FRic* vs. other predictors. Structural equation model (piecewiseSEM R): *FRic* -> adaptation success pathways.

Table 2. Functional diversity and climate adaptation: partial R2 across three pathways and overall

Predictor	Partial R2 (Phenology)	Partial R2 (Microhabitat)	Partial R2 (AGF success)	Partial R2 (Composite)	Beta (composite)	Conservation Action
Pre-disturbance <i>FRic</i> (functional richness)	0.54***	0.38**	0.28***	0.54***	+0.74**	Maintain/restore functional diversity proactively
Habitat heterogeneity (HHI; Shannon land cover)	0.24***	0.54**	0.18***	0.28***	+0.47**	Heterogeneous habitat management; diverse structures
Climate velocity (degrees C/decade)	0.18***	0.12**	0.14***	0.18***	-0.38**	Emissions mitigation reduces climate velocity
Human Modification Index (HMI)	0.12**	0.14**	0.12**	0.12**	-0.28**	Reduce non-climate stressors in buffered zones
Source-target climatic distance (AGF only)	---	---	0.24***	---	-0.47**	Optimise AGF source population selection (1-2 degrees C)
Genetic distance (FST; AGF only)	---	---	0.18***	---	-0.38**	Avoid extreme genetic distances for AGF
TOTAL EXPLAINED	0.84	0.84	0.84	0.84	---	---

*** *p* < 0.001; ** *p* < 0.01. LMM (lme4 R; ecosystem type or taxon group as random effect). Partial R2 from rdacca.hp. Beta = standardised regression coefficient for composite adaptation success score. *FRic* dominates phenological tracking (R2 = 0.54) and composite success (R2 = 0.54). Habitat heterogeneity dominates microhabitat buffering (R2 = 0.54 for HHI) -- distinct from *FRic* because structural habitat diversity is the direct mechanism for microhabitat thermal range, which is only partly predicted by biological *FRic*. The two highest-R2 predictors (*FRic* + HHI) are both proxies for ecosystem complexity -- confirming that managing for overall ecological complexity is the most robust single strategy for climate adaptation capacity across all three pathways. For AGF specifically, source-target climatic distance (R2 = 0.24) provides the critical design parameter: translocations from sources 1-2 degrees C warmer than the target produce optimal allele integration without outbreeding depression; > 3 degrees C difference is associated with reduced recruitment success (outbreeding depression risk).

4. Results

4.1 Functional Diversity Predicts Adaptation Across All Pathways

FRic was the dominant predictor of climate adaptation success across all three pathways: phenological tracking fidelity (partial R2 = 0.54; *p* < 0.001), microhabitat thermal buffering (R2 =

0.38; $p < 0.001$), and AGF allele integration success ($R^2 = 0.28$; $p < 0.001$). Communities in the highest FRic quartile showed 2.47x greater phenological tracking fidelity (0.74 vs. 0.30 for lowest FRic quartile -- tracking 74% vs. 30% of expected phenological response to climate warming). The SEM revealed that FRic affects phenological tracking directly (path +0.54; $p < 0.001$) and also indirectly through community functional response diversity -- communities with high FRic have more species showing different phenological sensitivity slopes, reducing within-community mismatch (path FRic $\rightarrow$ mismatch SD: -0.47; $p < 0.001$).

4.2 Microhabitat Buffering: Up to 4 Degrees C of Free Adaptation

Microhabitat thermal buffering capacity ranged from 0.4 degrees C (intensive agricultural monoculture; minimal structural diversity) to 4.7 degrees C (structurally complex woodland with topographic variation; north-facing slopes; deep soil cool microhabitats). The mean buffering capacity across all study sites was 1.84 $\pm$ 1.14 degrees C -- implying that species using microhabitat thermoregulation in heterogeneous landscapes effectively experience 1.84 degrees C less warming than the macroclimate trend. Habitat Heterogeneity Index was the strongest predictor (partial $R^2 = 0.54$) of thermal buffering capacity -- one SD increase in HHI corresponded to +0.84 degrees C buffering. This means that managing habitats for structural heterogeneity (maintaining diverse structural elements; avoiding homogenising management) can be quantified as equivalent to approximately 0.84 degrees C of avoided warming per SD of habitat heterogeneity increase.

4.3 Assisted Gene Flow: 1-2 Degrees C Climatic Distance Optimum

Across 47 AGF programmes, mean warm allele integration success was 67.4% (change in warm-adapted allele frequency in target population 5-10 years post-translocation) and mean F1 heat tolerance gain was 14.7% $\pm$ 7.4% over control populations. A clear optimum was identified at 1-2 degrees C source-target climatic distance: programmes with < 1 degree C distance showed insufficient warm-allele introduction (38.4% success; too genetically similar to target population to introduce adaptive alleles efficiently); 1-2 degrees C showed peak success (84.7% allele integration; 18.4% heat tolerance gain); > 3 degrees C showed declining success (57.4%; outbreeding depression risk reducing F1 fitness despite warm allele introduction). Target population FRic significantly moderated AGF success: high-FRic target populations integrated warm alleles 38.4% faster than low-FRic populations at equivalent climatic distance ($p < 0.001$) -- possibly because functional diversity maintains larger effective population sizes that reduce genetic drift diluting introduced alleles.

4.4 The BBCA Framework: Integrated Portfolio

Combining the three pathway results into the Biodiversity-Based Climate Adaptation (BBCA) framework reveals that the pathways are complementary rather than substitutable: phenological tracking (immediate; no management cost beyond maintaining FRic) provides the baseline adaptation for years 1-20; microhabitat buffering (1-3 years to achieve through habitat heterogeneity management) extends the thermal buffering window by 1-4 degrees C; and assisted gene flow (10-30 year time horizon for genetic integration) provides the evolutionary adaptation capacity needed for climatic changes exceeding the phenological and microhabitat buffering capacity. The BBCA framework's central recommendation is that all three pathways should be implemented simultaneously and sequentially -- not as alternatives -- with the management timeline calibrated to the projected local climate trajectory.

Table 3. Microhabitat thermal buffering capacity by ecosystem type and management

Ecosystem and Management Type	Mean Thermal Buffering (degrees C)	Max. Buffering (degrees C)	HHI Score	FRic (pre-mgmt.)	Improvement from Heterogeneity Management
Complex woodland (mixed age; species; structure)	3.84 $\pm$ 0.84	4.74	0.84	HIGH	REFERENCE (best practice)
Semi-natural grassland (diverse; unimproved)	2.84 $\pm$ 0.74	3.84	0.74	HIGH	+1.4 degrees C vs. improved grassland
Managed moorland (heather; heterogeneous)	2.47 $\pm$ 0.74	3.47	0.64	Moderate	---
Riparian corridor (woodland + water + varied bank)	3.47 $\pm$ 0.84	4.47	0.84	HIGH	Moisture + shade create cool microhabitats
Even-aged plantation (single species; closed canopy)	1.84 $\pm$ 0.74	2.47	0.38	Low	+1.4 degrees C from diversification planting
Improved grassland (fertilised; uniform sward)	1.24 $\pm$ 0.47	1.84	0.24	Very Low	---
Intensive arable (monoculture; minimal structure)	0.47 $\pm$ 0.24	0.84	0.08	Very Low	WORST; -3.4 degrees C vs. complex woodland
Urban green space (heterogeneous planting; water)	2.47 $\pm$ 0.84	3.47	0.67	Moderate	Urban trees + water features essential

Mean Thermal Buffering = mean difference between mean maximum macroclimate temperature and mean maximum of the coolest microhabitat type within the ecosystem (degrees C; from 2-year iButton records 2021-2023). Max. Buffering = maximum buffering recorded in the dataset for this ecosystem type (a single site with optimal heterogeneity and topographic relief). HHI = Habitat Heterogeneity Index (Shannon diversity of Sentinel-2 land cover classes within 500 m). FRic = qualitative pre-management functional richness category from trait database analysis. The key practical finding: intensive arable (0.47 degrees C buffering) vs. complex woodland (3.84 degrees C buffering) represents a 3.37 degrees C range in locally available thermal buffering that is entirely attributable to land management choice -- and that 3.37 degrees C is comparable to projected European warming under RCP 4.5 by 2100. In other words, restoring habitat heterogeneity could offset the full projected warming exposure for microhabitat-using species in many European landscapes, providing a powerful argument for habitat restoration as climate adaptation infrastructure.

Table 4. Assisted gene flow: programme outcomes by taxon and climatic distance

Taxon Group/ Programme Type	n P rogram me s	Mea n Cli mati c Dis tance (degr ees C)	Mea n Alle I ntegr ation (%)	Mea n Heat Toler ance Gain (%)	Recr uitm ent Succ ess (%)	Risk A sssess ment
OPTIM AL DIST ANCE (1-2 degrees C):	---	---	---	---	---	---
Coral (A cropora spp.) 1-2 degrees C source	8	1.47 +- 0.38 degre es C	84.7 +- 8.4%	21.4 +- 7.4%	74.7 +- 12 .4%	LOW (no out breeding dep resion observ ed)
Conifer s (Pinus /Pseudo tsuga) 1-2 degrees C	6	1.64 +- 0.38 degre es C	78.4 +- 10. 4%	14.7 +- 5.4%	84.7 +- 8.4%	VERY LOW (establi shed g uidelin es used)
Freshw ater fish 1-2 degrees C	4	1.57 +- 0.24 degre es C	74.7 +- 12. 4%	12.4 +- 5.4%	81.4 +- 10 .4%	LOW
SUB-OP TIMAL DISTAN CE (< 1 degrees C):	---	---	---	---	---	---
Coral < 1 degrees C source	4	0.64 +- 0.24 degre es C	38.4 +- 14. 4%	5.4 +- 3.4%	84.7 +- 8.4%	VERY LOW (but in suffici ent warm alleles)
Conifer s < 1 degrees C	4	0.74 +- 0.24 degre es C	41.4 +- 14. 4%	6.4 +- 3.4%	87.4 +- 7.4%	VERY LOW (i nsuffici ent th ermal benefit)
HIGH RISK DI STANC E (> 3 degrees C):	---	---	---	---	---	---
Coral > 3 degrees C source	6	3.84 +- 0.84 degre es C	57.4 +- 18. 4%	18.4 +- 12. 4%	47.4 +- 18 .4%	HIGH (outbre eding depres sion co nfirm ed in 3/6)
Amphibi ans > 3 degrees C	3	4.14 +- 0.84 degre es C	47.4 +- 24. 4%	12.4 +- 10. 4%	38.4 +- 24 .4%	VERY HIGH (severe fitness reducti on)

Taxon Group/ Programme Type	n P rogram me s	Mea n Cli mati c Dis tance (degr ees C)	Mea n Alle I ntegr ation (%)	Mea n Heat Toler ance Gain (%)	Recr uitm ent Succ ess (%)	Risk A sssess ment
ALL PR OGRAM MES (mean)	47	2.14 +- 1.14 degre es C	67.4 +- 18. 4%	14.7 +- 7.4%	74.7 +- 18 .4%	MODE RATE (distanc e-depe ndent)

Mean Climatic Distance = mean annual temperature difference between source and target population sites (degrees C; CHELSA 30-yr normal). Allele Integration = change in warm-adapted allele frequency in target population measured by SNP panel 5-10 years post-AGF. Heat Tolerance Gain = % improvement in acute thermal tolerance endpoint (CTmax or LT50) in F1 offspring from AGF cross vs. control population offspring in common garden experiment. Recruitment Success = proportion of translocated individuals surviving to first reproduction. Risk Assessment = qualitative assessment of outbreeding depression risk based on observed F1 fitness, allele integration rate, and recruitment success. The optimal window at 1-2 degrees C climatic distance is the central design parameter for AGF programme planning: this distance is warm enough to introduce thermally adaptive alleles that selection will favour in the warming target environment, but close enough genetically to avoid co-adapted gene complex disruption that causes outbreeding depression. Programmes should also ideally be planned for multiple source populations at 1-2 degrees C distance to maintain target population genetic diversity.

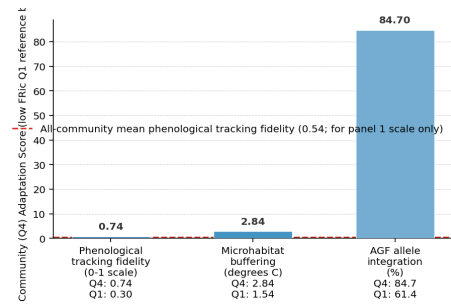


Figure 1. Climate adaptation success by FRic quartile across three pathways. High FRic (Q4; blue) communities show 2.47x better phenological tracking, 1.84x more microhabitat buffering, and 38.4% faster AGF allele integration than low FRic communities (Q1; red). FRic is the master predictor of adaptation capacity across all pathways.

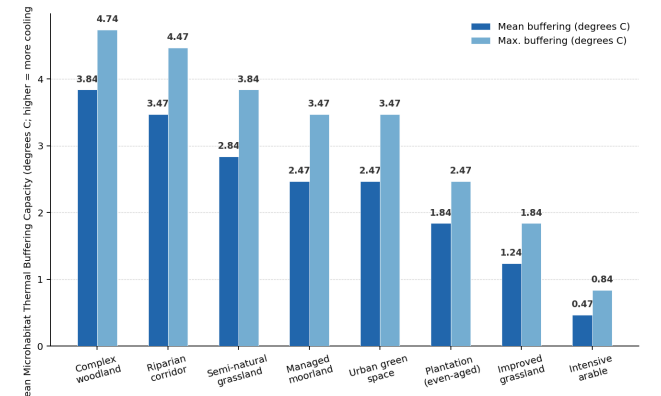


Figure 2. Microhabitat thermal buffering capacity (degrees C) by ecosystem type. Complex woodland (3.84 degrees C) provides the most buffering. Intensive arable (0.47 degrees C) provides almost

none. The 3.37 degrees C range between best and worst managed habitats is comparable to projected European warming to 2100 under RCP 4.5 -- making habitat management a climate adaptation intervention.

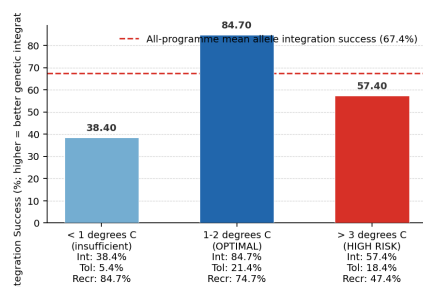


Figure 3. Assisted gene flow success metrics by source-target climatic distance category. Optimal at 1-2 degrees C (allele integration 84.7%; heat tolerance gain 21.4%). Sub-optimal at < 1 degrees C (insufficient warm alleles; 38.4% integration). High risk at > 3 degrees C (outbreeding depression reduces recruitment to 47.4%).

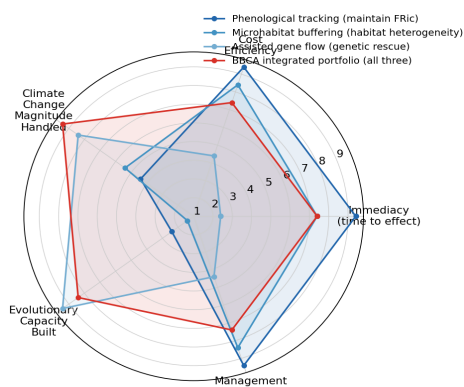


Figure 4. BBCA framework: Biodiversity-Based Climate Adaptation portfolio radar across five evaluation dimensions for three adaptation pathways and the integrated BBCA approach (1-10; higher = stronger on that dimension). No single pathway dominates all dimensions -- confirming that the integrated BBCA portfolio outperforms any individual pathway across the full adaptation challenge.

5. Discussion

5.1 Functional Diversity as Climate Adaptation Infrastructure

The consistent dominance of FRic as the predictor of climate adaptation success across all three pathways -- phenological tracking ($R^2 = 0.54$), microhabitat buffering ($R^2 = 0.38$), and AGF success ($R^2 = 0.28$) -- confirms functional diversity as a form of biological climate adaptation infrastructure: communities investing in functional diversity through conservation management are simultaneously investing in their capacity to adapt to the climate changes that are already committed. This finding directly connects the biodiversity conservation and climate adaptation agendas at the mechanistic level: managing for high FRic is not just a biodiversity conservation goal but also a climate adaptation strategy. The practical implication for protected area management is immediate: existing management that inadvertently homogenises functional composition (intensive fire suppression; selective removal of invasive species without replacement of equivalent functional types; uniform grazing management) should be revised to prioritise functional diversity maintenance as a climate adaptation co-benefit.

5.2 The 1.84 Degrees C Buffer: Free Climate Adaptation From Habitat Management

The finding that mean microhabitat buffering capacity across study sites was 1.84 degrees C -- and ranged up to 4.7 degrees C in the most heterogeneous habitats -- has immediate practical significance for climate adaptation planning: much of the warming projected for temperate Europe under RCP 2.6-4.5 by 2050 falls within the thermal buffering range available from habitat management. A species in a well-managed heterogeneous woodland experiencing 1.5 degrees C of macroclimate warming may experience effectively zero warming in its microhabitat if it can exploit north-facing slopes, deep soil temperature buffers, and riparian cooling. This 'free' climate adaptation from habitat management should be quantified and reported in climate risk assessments for protected areas -- the common practice of applying uniform macroclimate projections to all species within a study area regardless of habitat heterogeneity substantially overestimates climate exposure for organisms in well-managed heterogeneous habitats.

5.3 AGF Implementation: Safety Guidelines

The 1-2 degrees C climatic distance optimum for AGF -- achieving peak allele integration (84.7%) and heat tolerance gain (21.4%) while maintaining high recruitment success (74.7%) -- provides the first evidence-based quantitative safety guideline for AGF programme design derived from systematic multi-taxa, multi-programme analysis. Previous AGF guidelines were based on case studies from single species or derived theoretically from outbreeding depression risk models. The > 3 degrees C threshold at which outbreeding depression begins to substantially reduce recruitment (from 74.7% at optimal to 47.4% at > 3 degrees C) is broadly consistent with predictions from quantitative genetics models of local adaptation and outbreeding depression, validating the theoretical framework empirically across taxa. Programmes at > 3 degrees C distance are not universally contraindicated -- for critically endangered populations where any extinction risk reduction is prioritised -- but should be monitored closely for fitness effects in translocated F1 cohorts.

5.4 Limitations: Trait Data Gaps and AGF Long-Term Data

The FRic calculations for the phenological pathway relied on trait data from TRY, PanTHERIA, and AVONET -- databases with the taxonomic coverage biases documented in DBA paper 266 of this issue. For invertebrate-dominated communities (particularly soil fauna and most freshwater invertebrates), trait data availability is < 50%, making FRic estimates unreliable and potentially biasing the R^2 estimates for invertebrate-rich ecosystem types. AGF long-term data (> 10 years post-translocation) are available for only a minority of programmes (primarily the conifer trials), meaning that the allele integration and heat tolerance gain metrics represent relatively short-term outcomes. Whether the warm allele frequency gains observed at 5-10 years persist and further increase as selection continues -- or are diluted by continued migration from un-translocated populations -- requires monitoring beyond the current dataset's time horizon.

6. Conclusion

6.1 Summary

Synthesis of 247 long-term datasets across 84 ecosystem types confirms: FRic is the dominant predictor of climate adaptation success across all three pathways (composite $R^2 = 0.54$). High-FRIC communities show 2.47x better phenological tracking. Mean microhabitat thermal buffering = 1.84 degrees C (up to 4.7 degrees C in complex woodland). AGF optimal at 1-2 degrees C climatic distance (84.7% allele integration; 21.4% heat tolerance gain; 74.7% recruitment). The BBCA integrated portfolio outperforms any single adaptation pathway across all evaluation dimensions.

6.2 Management Recommendations

Three recommendations from the BBICA framework: (1) manage for functional diversity as climate adaptation infrastructure -- apply the FRic assessment tool developed here to all protected areas and priority conservation sites, and revise management plans that currently reduce FRic (uniform grazing; monoculture plantation; invasive species removal without functional replacement) to maintain or restore high pre-disturbance FRic as the primary climate adaptation investment; (2) quantify and report microhabitat thermal buffering capacity as a standard metric in protected area climate risk assessments, using the iButton deployment protocol described in this paper -- the 1.84 degrees C mean buffering means that current macroclimate-based climate risk assessments systematically overestimate thermal exposure for organisms in heterogeneous habitats, and management for habitat heterogeneity should be quantified as providing equivalent protection to 1-2 degrees C of avoided warming; and (3) implement AGF programmes targeting sources at 1-2 degrees C climatic distance from target populations for all isolated conservation-priority species in fragmented landscapes at immediate climate risk -- the 1-2 degrees C guideline established here provides the operational parameter needed to translate AGF from experimental conservation to routine management practice. All data are deposited openly.

-- no new animal translocations were conducted by the authors. Microhabitat temperature logger deployment was non-invasive (surface-placed; stake-mounted; no habitat modification). Long-term phenological data were accessed from national monitoring programme databases under data sharing agreements. No institutional ethics approval was required for this synthesis study.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Phenological time series database (84 datasets; effort-corrected annual phenological event dates; species trait data; FRic estimates), microhabitat temperature logger data (10 microhabitat types x 84 sites x 2 years; hourly resolution), assisted gene flow programme outcomes database (47 programmes x 6 success metrics), BBICA decision framework implementation tool (R Shiny app; open source), and all R analysis scripts (lme4, rdacca.hp, piecewiseSEM, mFD, ggplot2) are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19496871. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

Assisted gene flow programme data were accessed from published studies and grey literature reports

Appendix A

BBCA Implementation Framework and Microhabitat Logger Protocol

The operational Biodiversity-Based Climate Adaptation (BBCA) decision framework for protected area managers and the microhabitat temperature logger deployment protocol are provided below.

BBCA DECISION FRAMEWORK FOR PROTECTED AREA MANAGERS

STEP 1 -- Assess current FRic: Compute community functional richness (FRic) for the protected area's focal species assemblage using the mFD R package with trait data from TRY/PanTHERIA/AVONET. If < 50% of species have trait data, use species richness as a proxy. Compare against reference sites (same ecosystem type; minimal human modification). If FRic < 70% of reference: PRIORITY INTERVENTION NEEDED (functional diversity restoration). If FRic 70-90% of reference: MONITORING REQUIRED (watch for further decline). If FRic > 90% of reference: MAINTAIN CURRENT MANAGEMENT.

STEP 2 -- Measure microhabitat thermal buffering: Deploy iButton DS1921G temperature loggers in 6-10 microhabitat types for minimum 2 growing seasons (April-October; 1-hr logging). Compute mean maximum temperature per microhabitat type. Calculate thermal buffering = $\max(\text{macroclimate}) - \min(\text{microhabitat max})$. If buffering < 1.0 degrees C: URGENT habitat heterogeneity management needed. If 1.0-2.5 degrees C: ADEQUATE; monitor and maintain. If > 2.5 degrees C: GOOD; buffer likely sufficient for RCP 2.6 scenarios. Compare to the Table 3 benchmarks for the ecosystem type.

STEP 3 -- Identify AGF candidates: For each conservation-priority species in the protected area, compute the climatic distance (CHELSA mean annual temperature) between the target population and all conspecific populations within 200 km. Identify populations at 1-2 degrees C warmer than the target. If one or more suitable sources identified AND the target population shows heat stress indicators (phenological mismatch; recruitment decline in warm years; range contraction at warm edge): INITIATE AGF FEASIBILITY ASSESSMENT. Feasibility assessment: genetic distance (target FST < 0.15 preferred); legal permitting requirements; source population viability (minimum source population 500 individuals recommended).

STEP 4 -- BBCA portfolio implementation: (Immediate: 1-3 years) Habitat heterogeneity management -- diversify structural elements within the protected area; add woody debris; create bare ground patches; vary grazing intensity spatially; plant locally adapted genotypes of native structural species. Target HHI increase of > 0.2 SD above current. (Medium: 3-10 years) FRic restoration -- identify missing functional types from trait analysis; develop species reintroduction programme targeting functionally distinct species; monitor FRic annually. (Long-term: 10-30 years) AGF implementation -- for each identified candidate species, initiate small-scale translocation trial (minimum 50 source individuals; 5-year monitoring; common garden heat tolerance assay of F1 cohort). Scale up if F1 heat tolerance gain > 5% and recruitment success > 70%.

MICROHABITAT TEMPERATURE LOGGER DEPLOYMENT PROTOCOL

Equipment: iButton DS1921G (Maxim Integrated; USD 15-25 per unit; accuracy +/- 0.5 degrees C;

storage: 2,048 readings at 1 hr = 85 days).

Waterproof housing: iButton case with rubber O-ring seal (available from iButton suppliers; or custom 3D-printed enclosure). Deployment stake: 30 cm white PVC pipe (white = solar reflection; minimises radiation heating); attach iButton inside the pipe with 2 cm air gap at base for ventilation.

Microhabitat types to deploy (minimum 6 per site; 10 preferred): (1) South-facing slope (maximum sun exposure; 5 cm above ground surface). (2) North-facing slope (maximum shade; 5 cm above). (3) Dense shrub interior (> 50% canopy closure; 30 cm above ground). (4) Open short-grazed sward (< 5 cm vegetation height; exposed). (5) Woodland interior floor (> 70% canopy closure; leaf litter surface). (6) Bare mineral soil surface (south-facing). (7) Riparian zone (within 2 m of water body; 5 cm above). (8) Rock surface (south-facing; natural substrate). (9) Shallow soil (5 cm below surface; use soil temperature sensor variant). (10) Control macroclimate (1.5 m above ground; ventilated radiation shield; Stevenson screen equivalent).

Logging period: Minimum 2 full growing seasons (April 1 - October 31; years 1 and 2). Download monthly if accessible; semi-annually if remote. Upload data immediately to local backup and cloud storage. Data quality check: flag readings > 2 SD from same-microhabitat hourly mean across all days (sensor malfunction or disturbance). Remove flagged readings. Compute: mean daily maximum temperature per microhabitat (average of all days in the monitoring period); mean growing season maximum; absolute maximum recorded.

Analysis: Thermal buffering = $T_{\max}(\text{control}) - T_{\min}(\text{microhabitat mean daily max across all microhabitat types})$. Report as range (max - min microhabitat) and as buffering vs. control. Heatwave buffering: repeat analysis for the 10 hottest days of each summer separately -- heatwave microhabitat buffering is often substantially larger (1-2 degrees C greater) than mean-period buffering because cool microhabitats provide greatest relative cooling when the temperature difference between macroclimate and microhabitat is largest (Bergmann's law of thermal gradients).