Tansley Review Submission

Predictive Evolutionary Genomics: Principles, Validation, and Practice

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Abstract

Contemporary evolution occurs on observable timescales, enabling prospective evolutionary forecasting with quantitative frameworks rather than only retrospective inference. We propose a unified probabilistic framework that integrates three approaches linked to detectability windows through time. Trait-based models use multivariate quantitative-genetic equations to project correlated phenotypic responses over ~5–20 generations while the G-matrix is locally stable. Allele-based analyses model frequency dynamics at identifiable loci over ~20–100 generations, when selection outpaces drift and sampling error. For longer horizons, composite adaptation scores aggregate many small effects to support 100+-generation projections under novel environments. These windows reflect detectability and parameter stability, not genetic architecture. Bayesian inference integrates genomic, phenotypic, and environmental evidence to yield probabilistic predictions with explicit uncertainty. Experimental evolution, historical herbarium series, and reciprocal transplants provide independent validation of forecast skill and transferability. Validated forecasts can guide conservation programs (genomic vulnerability and assisted gene flow), breeding programs (multi-generational, climate-aware selection), and ecosystem management (species-composition planning). By quantifying and propagating uncertainty, this programme shifts evolutionary biology from largely descriptive synthesis toward predictive practice.

I. Recent Advances in Evolutionary Prediction

Why now, and why it matters

The evolutionary changes we track today often unfold within the lifespan of our experiments (Lenski et al. 1991; Good et al. 2017; Tenaillon et al. 2016). Because we can assay genomes, phenotypes and environments at fine temporal resolution, we no longer observe evolution from the sidelines: we can study its mechanisms as they operate. Evidence for rapid evolutionary change spans diverse taxa: Darwin's finches reshaped their beak and body sizes over six drought-driven generations (Grant & Grant 2002), plant mating systems shifted toward selfing within decades as pollinators declined (Thomann et al. 2015), and Lenski's *Escherichia coli* lines accumulated adaptive mutations within a few years (Lenski et al. 1991). Other clear examples of the speed of evolution occur in crop pests that have evolved pesticide resistance faster than chemists can deploy new chemistries to control them (Gould et al. 2018), and in annual plants that are shifting flowering time in response to drought (Franks et al. 2017). Biological and experimental timescales have converged, creating possibilities and requirements. Possibility, because real-time data let us test quantitative forecasts against a moving target. Necessity, because management decisions, from biodiversity conservation to crop protection, must anticipate adaptive change for a more resilient society.

Evolution acts through hierarchical levels of organization: nucleotide changes alter proteins, proteins alter pathways, pathways alter traits, and traits alter fitness (James et al. 2023). Communities and biomes further aggregate these levels of organization into systems that we continually try to manage (Ball et al. 2009; Moilanen et al. 2009) and protect (IUCN 2013, Possingham et al. 2006). Mapping information spanning these levels remains challenging (Hasin et al. 2017). For decades, biological research has fallen into a "certainty trap," where researchers assumed that exhaustive mechanistic knowledge would automatically yield deterministic forecasts (Beatty, 1990). Other epistemological approaches suggest otherwise. Systems biology and ecological research demonstrate that when interactions are many, detailed mechanisms alone may not suffice for prediction (May, 1972; Grimm & Railsback 2005; Alon, 2019), yet they remain invaluable because they provide the levers for manipulating and validating models that consider higher levels of organization (Kitano, 2002). We need not abandon mechanism; rather, we must let it create rules while embracing the inherent uncertainty of biological systems.

Importantly, all evolutionary forecasting approaches share a common currency: fitness. Whether tracking phenotypic responses through the breeder's equation, monitoring allele frequencies via selection coefficients, or integrating polygenic effects, each method ultimately predicts fitness consequences through different mechanistic lenses. This unified perspective anchors our probabilistic framework.

Technological and Conceptual Convergence

Several interconnected advances have converged to make evolutionary forecasting feasible today. Genomic technologies now provide comprehensive views of genetic variation at population scales (Ellegren, 2014; Goodwin et al. 2016), revealing the raw material that constrains and enables evolutionary responses with unprecedented resolution (Allendorf et al. 2010). Computational advances enable Bayesian frameworks that embrace rather than eliminate uncertainty, treating probabilistic predictions as valuable information through integration of empirical data with evolutionary theory (Aguirre et al. 2014; Beaumont, 2010; Gelman et al. 2013). Perhaps most importantly, the maturation of long-term ecological studies and experimental evolution programs provides temporal validation datasets for testing forecasts against independent outcomes, transforming evolutionary prediction from theoretical exercise to empirically grounded science (**Box 2**; Kawecki et al. 2012; Exposito-Alonso et al. 2019; Wilkinson et al. 2021).

These technological advances reflect a broader philosophical transformation in the field. Evolutionary biology increasingly embraces its inherently probabilistic nature rather than pursuing deterministic approaches (Noble, 2012). Researchers are shifting from asking "Will this population adapt?" to asking "What is the probability of adaptation, with what confidence bounds, and over what time horizon?" Evolutionary prediction is becoming an empirically testable science (Nosil et al. 2020) increasingly adopted across a wide range of taxa (**Table 1**). This shift from seeking certainty to precise quantification of uncertainty enables practical applications of evolutionary forecasting now emerging in conservation and agriculture (Capblancq et al. 2020; Wortel et al. 2023).

One consequence of biological organization is that predictive breakthroughs emerge from recognizing that evolution shows scale-dependent predictability: outcomes can be more predictable than the mechanisms producing them (Noble, 2012; Tenaillon, 2014). Evolution confounds the normal relationship between mechanistic understanding and predictive power that characterizes most physical sciences (Beatty, 1990), though recent advances are improving our capacity to predict contemporary evolutionary change (Nosil et al. 2020). Unlike Newtonian systems where better mechanism characterization improves prediction quality, evolutionary systems can have well-characterized mechanisms yet remain unpredictable due to their combinatorial complexity (Kauffman, 1993; Orr, 2005; Wagner, 2005). This complexity often resolves at higher scales, where many lower-level contingencies average out to reveal predictable patterns, such as when we measure heritability and other quantitative genetic parameters (Walsh & Lynch, 2018), summarize evolutionary processes into rates (Haldane, 1949; Gingerich, 2009), or organize variation into categories whose relative abundance becomes predictable. Influenza surveillance demonstrates this principle, predicting the dominant global lineage a year ahead with ~93% accuracy despite stochastic mutation processes that underlie the emergence of each lineage (Luksza & Lässig, 2014).

Although evolutionary patterns may be more predictable than underlying mechanisms, mechanistic detail remains necessary for two reasons. First, it sharpens the priors of statistical models (Gelman et al. 2013): knowing which genes regulate flowering time or drought response (Andrés & Coupland, 2012; Shinozaki & Yamaguchi-Shinozaki, 2007) guides the choice of covariates and constrains parameter space. Second, it offers actionable entry points for intervention such as assisted gene flow (Aitken & Whitlock, 2013), or targeted breeding (Meuwissen et al. 2001), all of which operate at molecular or physiological scales (Heath et al. 2016). Our goal is to build forecasts that are informed by, and feed back to, actionable mechanisms at higher levels of organization.

Theoretical Foundations and the Certainty Trap

Nearly a century ago, Fisher, Wright, and Haldane built the mathematical foundations of evolutionary prediction (**Figure 1**), providing equations that linked mutation, drift, and selection to measurable population changes (Fisher, 1918; Wright, 1932; Haldane, 1927). Fisher's infinitesimal model captured how randomness permeates inheritance of complex traits (Fisher, 1918), while Wright formalized how genetic drift creates stochasticity even without environmental change (Wright, 1931). Haldane developed methods for estimating fixation probabilities of new alleles (Haldane, 1927), presaging our current ability to study the genetics of adaptation (Nosil et al. 2018). These contributions established evolutionary biology's quantitative foundations, yet reliable forecasts of evolutionary change remained elusive until the genomics era (Berg & Coop, 2014; Fuller et al. 2020). This early wave of prediction reveals a philosophical problem that affected evolutionary biology for decades: the relentless pursuit of certainty in an inherently uncertain process (Beatty, 1990).

The genetic variance-covariance matrix (***G***-matrix) exemplifies this certainty trap. Classical quantitative genetics treated the ***G***-matrix as an unchanging parameter that captures a population's evolutionary potential through genetic variances and correlations (Falconer & Mackay, 1996)—measure it once, apply it indefinitely. But real populations violate this assumption continuously. Selection eliminates beneficial variation, recombination reshuffles alleles, mutations introduce new variance, and genetic drift injects random fluctuations (Jones et al. 2007; Walsh & Lynch, 2018). The matrix's reliability thus degrades predictably over time, creating a natural temporal horizon of ~ 5-20 generations for trait-based predictions—not as a methodological limitation but as a biological reality. To create robust frameworks for predictive evolutionary genomics, we must account for these dynamic uncertainties rather than assuming static parameters (**Box 1**; Arnold et al. 2008).

Similarly, Wright's adaptive landscape maps fitness as topography: genotypes occupy positions, elevation equals reproductive success (Wright, 1932). Populations evolve by climbing peaks through genetic changes that increase fitness. Valleys represent maladaptive combinations that selection eliminates. Wright envisioned landscapes whose peaks and valleys rise and fall over time, yet generations of biologists applied his framework as fixed topographies—mountains and valleys through which populations climb toward unchanging peaks. This static interpretation simplified analysis but missed a truth: both landscape and population evolve simultaneously. Simpson developed Wright's dynamic perspective, explicitly emphasizing landscapes that change as environments shift (Simpson, 1944), yet this view remained largely theoretical due to measurement complexity on interactive genotypic surfaces (Gavrilets, 2004). Climate change makes this recognition essential. Populations now navigate landscapes that shift faster than adaptation can track the "peaks."

The remainder of the paper develops a scale-integrated framework for predictive evolutionary genomics. We overview three forecasting approaches that match research questions to different biological scales and levels of uncertainty (**Figure 2**), show how to combine these approaches using Bayesian methods that quantify uncertainty (**Figure 3**), and provide implementation guidelines. We emphasize that mechanistic understanding is necessary to improve predictive accuracy.

II. Three Complementary Forecasting Approaches

Matching methods to biological scales

Why are outcomes often more predictable than the mechanisms producing them? This question drives evolutionary forecasting and requires methods that work with biological hierarchies rather than applying uniform approaches to different organizational scales (Tenaillon, 2014; Beatty, 1990).

Consider three contrasting examples that illustrate this principle. At the phenotypic scale, trait correlations and genetic constraints create predictable evolutionary trajectories that emerge from underlying genomic complexity we need not fully characterize. The Breeder's equation drives crop variety development of desired phenotypes using pedigrees, trait scores and macro-parameters like selection intensity and heritability (Lush, 1937; Falconer & Mackay, 1996). At the genomic scale, individual loci experiencing selection pressures can be tracked through allele frequency changes (Haldane, 1927; Wright, 1931), regardless of broader phenotypic outcomes. Yet identifying a gene that controls a fraction of trait variation, which in turn controls a fraction of fitness variation, illustrates how compounding fractions limit our ability to forecast evolution from single genes (Rockman, 2012). At the polygenic scale, hundreds of small-effect variants collectively determine adaptive capacity through distributed effects that neither trait-based nor single-locus approaches can capture in isolation. The challenge lies in identifying causal alleles and tracking their evolution accurately (Schlötterer et al. 2015), but models are emerging (Boyle et al. 2017).

Instead of seeking one optimal forecasting method, we encourage researchers to use complementary approaches that target different biological hierarchies (**Figure 2**). These methods naturally stratify across temporal scales—not by arbitrary choice but because genetic architecture determines when evolutionary signal becomes detectable above noise (**Box 1**). Major-effect alleles produce rapid, trackable changes; polygenic architectures require longer timescales for signal integration; and quantitative genetic parameters remain reliable only while genetic covariances persist. Rather than viewing this as a limitation, we exploit these emergent patterns by matching analytical methods to the scales where biology creates predictability (Beaumont, 2010).

Trait-Based Approaches: Leveraging Phenotypic Predictability

Trait-based approaches apply the multivariate breeder's equation $\Delta \boldsymbol{z} = \boldsymbol{G}\beta$ to predict correlated responses from multiple traits simultaneously, leveraging $\boldsymbol{G}$-matrix relationships established in quantitative genetic studies (Lande, 1979). These approaches excel when genetic constraints are well-characterized and selection gradients can be estimated reliably from field studies, typically excelling over a few generations (5-20, Walter & McGuigan 2023). Modern genomic approaches are changing our ability to detect correlational selection from multiple traits simultaneously, providing the empirical foundation necessary for multivariate evolutionary forecasting (Svensson et al. 2021). When selection favors increased drought tolerance in crop plants, established $\boldsymbol{G}$-matrix relationships reveal whether populations can evolve in that direction or whether genetic correlations will deflect responses toward unexpected phenotypic combinations. Recent experimental work confirms that the direction of phenotypic evolution can be predicted from the alignment between selection gradients and genetic constraints (Mallard et al. 2023).

The approach's predictive power emerges from its ability to capture evolutionary constraints through the genetic variance-covariance matrix $\boldsymbol{G}$, which determines both the magnitude and direction of evolutionary responses regardless of selection's intended targets. Empirical studies demonstrate that evolvability metrics derived from $\boldsymbol{G}$-matrix structure can successfully predict the magnitude of phenotypic divergence in plant populations (Opedal et al. 2023). These constraint patterns often display consistency from related species and environments, providing foundations for forecasting when genetic architecture remains relatively stable (Lande, 1979; McGlothlin et al. 2018). For example, population divergence in *Eucalyptus globulus* follows predictable genetic lines of least resistance over geographic gradients (Costa e Silva et al. 2020). However, this consistency depends critically on $\boldsymbol{G}$-matrix stability.

The magnitude of variation in mutational covariance structures affects the stability of evolutionary predictions over many generations (Mallard et al. 2023). Dynamic treatment of genetic architecture dramatically extends forecast horizons because models continuously update genetic constraints as integral parts of the prediction process rather than treating them as static inputs. Each generation brings not only observable trait changes (Franks et al. 2007) but simultaneous constraint evolution (McGlothlin et al. 2018), an evolutionary dynamic that static approaches miss entirely (Blows & Hoffmann, 2005).

Trait-based approaches achieve optimal performance for short-term predictions spanning 5-20 generations, where $\boldsymbol{G}$-matrix constraints dominate evolutionary responses more strongly than demographic stochasticity or mutational input (Lande, 1979). Implementation demands extensive phenotypic data collected in multiple controlled conditions, requiring multi-environment phenotyping for adequate statistical power (Kawecki & Ebert, 2004). This data intensity limits applicability primarily to model systems or economically important crops where such experiments remain logistically feasible (**Table 2**; Walsh & Lynch, 2018).

Allele-Based Approaches: Mechanistic Genomic Insights

Allele-based approaches track frequency changes at individual loci through population genetic relationships that connect selection pressures to allele frequency changes (Barton & Turelli, 1989). These approaches perform optimally when genetic architecture involves relatively simple inheritance patterns with major-effect loci, or when polygenic architectures are characterized in multiple environments and populations. These methods suit medium-term forecasts spanning 20-100 generations (Schlötterer et al. 2015), effectively tracking beneficial mutations as they move through intermediate frequencies toward fixation while maintaining sensitivity to demographic and environmental factors influencing selection intensity (Wright, 1931; Lenski et al. 1991).

Contemporary genomic approaches provide sophisticated tools for estimating functional relationships between genetic variation and environmental gradients that drive natural selection throughout the landscape. Genotype-environment association (GEA) approaches scan entire genomes to identify loci whose frequencies vary predictably with environmental gradients, providing direct empirical estimates of how selection acts over geographic space while revealing environmental dependencies that likelihood functions require for reliable parameter estimation (Rellstab et al. 2015). Gradient forests extend this analytical logic by modeling nonlinear responses and complex interactions among multiple environmental variables, capturing the complex ways that climate, soil chemistry, and biotic factors jointly influence adaptive evolution through emergent selection pressures that simple correlation analyses cannot detect (Ellis et al. 2012). Whole-genome prediction models adopt a complementary strategy, using dense marker information to predict phenotypic outcomes spanning diverse environments, thereby revealing genetic architecture underlying adaptation while providing effect size estimates necessary for composite adaptation score approaches (Fitzpatrick & Keller, 2015).

Implementation requires genome-wide variant data, typically one million or more high-quality SNPs, combined with environmental associations strong enough to provide reliable estimates of selection coefficients (Rellstab et al. 2015; Goodwin et al. 2016). Predictive effectiveness diminishes for highly polygenic traits where distributed effects on many loci create evolutionary responses that individual locus models cannot capture adequately (Boyle et al. 2017; Barghi et al. 2019). Exceptions include chromosomal inversions that aggregate polygenic effects into superloci (Rieseberg, 2001; Ortiz-Barrientos et al. 2002; Battlay et al. 2025; Huang et al. 2025). Capture of adaptive alleles appears common in nature (Noor et al. 2001, Ortiz-Barrientos et al. 2002; Huang & Rieseberg, 2020) and suggests that allele-based approaches should be complemented with structural variation studies that can identify such chromosomal rearrangements (Wellenreuther & Bernatchez, 2018).

Composite Adaptation Score Approaches: Integrating Polygenic Architecture

Composite adaptation score approaches integrate information from thousands of loci simultaneously through weighted sums of variants, where each variant contributes to the score according to its estimated effect size and current frequency, capturing the distributed genetic architecture underlying complex trait evolution (Bay et al. 2017; Fitzpatrick & Keller, 2015). This polygenic method acknowledges that most ecologically important traits—drought tolerance, flowering time, thermal adaptation—arise from coordinated shifts from hundreds of genetic variants rather than dramatic changes at single loci (Barghi et al. 2019). This polygenic perspective is valuable for predicting responses to environmental conditions that lie outside historical experience, where individual loci provide insufficient predictive signal but coordinated response from many variants can reveal clearer adaptive trajectories.

Composite approaches prove most valuable for complex genetic architectures involving many small-effect loci, medium- to long-term projections exceeding 50-100 generations that require polygenic integration, and novel environmental conditions where individual loci provide insufficient predictive signal. These methods work effectively for quantitative traits like growth rate, stress tolerance, and reproductive timing that display continuous rather than discrete variation patterns (Barghi et al. 2019). Composite score methods have demanding data requirements, including genome-wide effect size estimates from association studies that typically rely on thousands of individuals to achieve adequate statistical power (Crossa et al. 2017; Exposito-Alonso et al. 2019). The computational intensity, combined with assumptions about effect size constancy and additivity in multiple environments, makes implementation challenging for natural systems where such datasets remain unavailable. Perhaps more challenging is moving from interpreting biological systems as simple sums of effects to systems where interactions among genes, like in genetic networks (Boyle et al. 2017; O'Brien et al. 2024), define evolutionary trajectories with mechanisms that we can understand and leverage for forecasting.

Distinguishing Prediction from Distance Metrics

While genomic offset methods measure current maladaptation—the distance between populations and environmental optima (Fitzpatrick & Keller, 2015; Capblancq et al., 2020)—evolutionary forecasting predicts trajectories toward those optima. Distance does not determine destiny: populations with large genomic offset may harbor sufficient genetic variation for rapid adaptation (Bay et al., 2017), while those with small offset may lack evolutionary potential (Exposito-Alonso et al., 2019). Genomic offset provides valuable initial screening to identify populations requiring detailed predictive analysis but cannot forecast evolutionary outcomes. Our framework explicitly models the dynamic processes—genetic constraints, selection gradients, and demographic factors—that determine whether and how populations traverse fitness landscapes toward new optima. Operationally, many GO implementations are polygenic scores of environment-associated alleles; when calibrated against observed fitness they become polygenic fitness scores, which belong in the forecasting pipeline rather than as stand-alone distances.

Integrative Framework for Scale-Dependent Prediction

These three complementary approaches—trait-based methods leveraging $\boldsymbol{G}$-matrix constraints, allele-based approaches tracking genomic mechanisms, and composite scores integrating polygenic architecture—represent different analytical lenses for viewing the same underlying evolutionary process rather than competing methodological paradigms. The power emerges from recognizing that biological organization creates natural scales of predictability that we can exploit systematically (Lande, 1979; Walsh & Blows, 2009; Wortel et al. 2023).

Scale-dependent predictability operates through several mechanisms. At the trait level, genetic correlations and constraints create predictable trajectories even when underlying genomic mechanisms remain complex (Lande, 1979; Arnold et al. 2008; Walter et al. 2018). Individual loci can be tracked precisely when their effects are large enough to overcome demographic noise and when environmental associations can be measured reliably (Wright, 1931; Barton & Turelli, 1989; Schlötterer et al. 2015). Polygenic architectures become predictable when we integrate over enough variants to average out individual locus uncertainty, particularly under novel environmental conditions where aggregated effects, even if scattered across the genome, can be more reliable than single-locus predictions (Boyle et al. 2017; Barghi et al. 2019; Capblancq et al. 2020).

Each approach optimizes prediction accuracy for different biological scales and data availability scenarios. Trait-based methods predict phenotypic responses through genetic constraints, allele-based approaches reveal mechanistic pathways driving adaptation, and composite scores capture polygenic architecture underlying complex trait evolution. When data permit multiple approaches, integration provides robust uncertainty quantification while revealing which biological scales drive predictable responses (Beaumont 2010; Csilléry et al. 2010; Gelman et al. 2013). Rather than choosing between approaches, we select the combination that best matches our biological system, available data, and forecasting objectives (**Box 1**). This scale-dependent framework leads naturally to a unified probabilistic foundation that coordinates these diverse approaches and transforms their outputs into coherent, actionable predictions with explicit uncertainty bounds—our next focus.

The take home message is that time is not architecture. The windows we assign (5–20, 20–100, 100+) are detectability and parameter-stability regimes, not statements about mono- vs polygenicity. Any architecture can be analysed on any timescale provided the relevant parameters are identifiable and calibrated.

III. The Probabilistic Framework

Unifying theory behind the three approaches

The three forecasting approaches—trait-based, allele-based, and composite scores—share a common foundation rooted in Bayesian inference. This framework transforms raw genomic, phenotypic, and environmental observations into distributions of evolutionary futures (**Figure 3**). Rather than seeking single-point predictions, the approach quantifies uncertainty by treating each evolutionary parameter as a random variable that updates as empirical evidence accumulates (Beaumont, 2010; Gelman et al., 2013). In practice, $\boldsymbol{\beta}$ (trait selection gradients), s (locus-specific selection), and polygenic fitness scores are all likelihood terms about $\boldsymbol{w}$, so the posterior is “probability of future fitness paths given $\boldsymbol{\beta}$, s, and polygenic effects under $E(t)$”.

The mathematical foundation applies regardless of which forecasting approach we employ:

$$P(Future|Data, Environment) \propto P(Data|Parameters, Environment) \times P(Parameters)$$

This expression captures how fitness, the common currency across all approaches, manifests at different biological scales within our Bayesian framework. The likelihood function encodes fitness consequences whether measured through phenotypic selection gradients (β), allele-specific selection coefficients (s), or integrated polygenic effects. The expression thus reveals the logic of evolutionary forecasting: beliefs about future evolutionary trajectories (posterior) emerge from combining empirical evidence (likelihood) with theoretical understanding (prior), conditioned on environmental context. This approach transforms biological observations into risk assessments with explicit uncertainty bounds, making fitness both the biological currency and the prediction target unified through Bayesian inference.

Stage 1: Constructing the Likelihood Function

Forecasting begins by constructing a sampling model that links observed biological patterns to underlying evolutionary processes:

$$P(D|A, E)$$

This likelihood function contains the empirical foundation of evolutionary forecasts. The data component D represents genomic and phenotypic observations: allele frequencies sampled across populations and environments, trait measurements from common garden experiments, fitness estimates from field studies, and environmental associations detected through landscape genomics. The adaptive parameters A capture unobserved evolutionary forces: selection gradients acting on traits, genetic covariance structures linking traits and constraining responses, demographic parameters governing population dynamics, and genetic interactions determining how populations respond to environmental challenges. The environmental component E encompasses environmental conditions that drive natural selection: temporal variance in temperature and precipitation, extreme event frequency and intensity, soil chemistry gradients creating microhabitat heterogeneity, and disturbance regimes reshaping fitness landscapes across space and time.

Stage 2: Bayesian Integration and Uncertainty Propagation

The likelihood function captures one component of the evolutionary story. To generate actionable forecasts, researchers must combine empirical evidence with broader understanding of evolutionary processes through prior distributions that formalize decades of quantitative genetic research establishing typical heritability ranges, common garden experiments revealing phenotypic plasticity magnitudes and environmental dependence, meta-analyses providing baseline demographic rates across related species, and theoretical population genetics supplying principles about relationships between effective population size, selection intensity, and natural selection efficacy (Falconer & Mackay, 1996; Walsh & Lynch, 2018).

Bayes' theorem provides the mathematical machinery for combining prior knowledge with empirical evidence:

$$P(A|D,E) \propto P(D|A,E) \times P(A)$$

The resulting posterior distribution $P(A|D,E)$ represents updated beliefs about adaptive parameters after incorporating all available empirical evidence. Rather than collapsing this probabilistic information into point estimates, the Bayesian framework preserves entire distributions that capture remaining uncertainty about selection gradients, genetic variances, demographic rates, and all other parameters influencing evolutionary outcomes.

<u>Dynamic genetic architecture</u>

The framework treats every element of genetic architecture as a dynamic stochastic variable rather than a static parameter. This acknowledges that the genetic variance-covariance structure constraining evolutionary responses itself evolves:

$$\boldsymbol{G}_{ij}(t+1) = \boldsymbol{G}_{ij}(t) + \Delta\boldsymbol{G}_{selection} + \Delta\boldsymbol{G}_{drift} + \Delta\boldsymbol{G}_{mutation} + \Delta\boldsymbol{G}_{recombination}$$

This dynamic treatment extends meaningful forecast horizons because models continuously update genetic constraints as part of the prediction process rather than treating them as static inputs estimated once and applied indefinitely. Each generation brings observable trait changes and simultaneous constraint evolution—an evolutionary dynamic that static approaches miss entirely (Blows & Hoffmann, 2005).

Stage 3: Computational Implementation and Validation

The computational challenge lies in efficiently sampling from high-dimensional posterior distributions spanning thousands of genetic and demographic parameters while maintaining mathematical rigor for reliable uncertainty quantification. The choice of computational approach depends on the complexity of the likelihood function and the speed requirements of the application.

When posterior distributions can be evaluated directly, Markov Chain Monte Carlo (MCMC) methods provide the most rigorous approach. Algorithms like Metropolis-Hastings explore posterior landscapes by generating samples that converge to true posterior distributions (Gelman et al., 2013). Although computationally intensive, these methods excel when likelihood functions can be computed exactly because they enable precise parameter uncertainty characterization without approximation.

However, many evolutionary models involve demographic complexity or polygenic architectures that make likelihood calculations mathematically intractable. In these cases, Approximate Bayesian Computation (ABC) bypasses the likelihood entirely through forward simulation (Beaumont, 2010). Rather than computing probabilities directly, ABC generates synthetic datasets by simulating evolutionary processes under proposed parameter values, then assigns high posterior weight to parameters producing synthetic data that closely match observed patterns. Modern implementations enhance efficiency by using machine learning to identify informative summary statistics that capture the most relevant aspects of the data for parameter estimation.

When computational speed becomes critical—such as in real-time forecasting applications or ensemble approaches requiring hundreds of independent model runs—Variational Bayes offers a faster alternative by trading some approximation accuracy for dramatic speed gains (Gelman et al., 2013). Instead of sampling from the full posterior complexity, this approach finds simpler distributions that approximate the true posterior shapes. Although less precise than MCMC, Variational Bayes scales effectively to thousands of parameters while providing uncertainty estimates orders of magnitude faster, making it particularly valuable when rapid results are needed for management decisions.

Unified Foundation for Evolutionary Prediction

This probabilistic framework provides mathematical and conceptual unity underlying all three forecasting approaches by establishing common foundations for uncertainty quantification, prediction validation, and adaptive learning from forecast errors. Whether researchers track $\boldsymbol{G}$-matrix evolution, monitor allele frequency changes, or calculate polygenic adaptation scores, the framework ensures that all forecasts provide appropriately calibrated assessments of confidence and risk that can guide evidence-based conservation and management decisions.

The practical implementation of this framework across biological systems, data types, and management applications forms the foundation for transforming evolutionary prediction from academic exercise to operational infrastructure for managing life on a changing planet. Our next section translates these principles into implementation guidelines that researchers and managers can deploy immediately.

IV. From Data to Implementation: Matching Requirements to Forecasting Approaches

Strategic decision framework for evolutionary forecasting

Evolutionary forecasting requires strategic decisions that match biological questions, available resources, and data constraints to appropriate analytical approaches. Rather than overwhelming practitioners with data requirements, this section provides guidance on essential elements that can expand analytical capability for evolutionary forecasting, as resources permit. The first decision determines everything else: how far into the future do you need to predict, and under what environmental scenarios? Your forecasting horizon shapes both the biological questions you can address and the data requirements you must meet. This temporal dimension directly connects to our three-scale framework because different approaches excel at different time horizons while requiring distinct data architectures. The second strategic decision involves resource allocation among data collection, analytical development, and validation activities. Most studies lack adequate sample sizes or environmental coverage for their chosen approach. When data are insufficient, the axiom is to collect more data, but in its absence simpler models can be the better solution rather than forcing complex approaches onto inadequate datasets.

Essential data architectures for each approach

Trait-Based Forecasting: Phenotypic Infrastructure Requirements

Trait-based evolutionary forecasting through the multivariate breeder's equation requires phenotypic characterization that captures both genetic variance-covariance structure $\boldsymbol{G}$-matrix) and selection gradients (β) operating in multiple correlated traits simultaneously. Statistical requirements are substantial: detecting genetic correlations between traits typically requires minimum sample sizes of 100-200 genotypes measured in multiple environments to achieve adequate precision to determine evolutionary constraints (Lynch & Walsh, 1998). Common garden experiments provide the empirical foundation by growing genetically diverse individuals under controlled conditions that separate heritable genetic effects from environmental plasticity. The experimental design must span sufficient environmental variation to estimate selection gradients while maintaining replication adequate for $\boldsymbol{G}$-matrix estimation. In practice, this typically demands growing 100+ genotypes in 3-5 environments with 5-10 replicates per genotype-environment combination.

High-throughput phenotyping platforms address data collection constraints by capturing thousands of trait proxies through automated imaging systems. Drone-based multispectral flights can record spectral signatures encoding information about photosynthetic capacity, water status, nitrogen content, and stress responses in hundreds of individuals in single flights (Shakoor et al. 2017). This approach enables replacing labor-intensive measurements on limited individuals with multispectral indices capturing population-scale variation. Selection gradient quantification requires fitness measurement spanning environmental gradients that capture selective pressures operating in natural populations. Direct fitness measurement through lifetime reproductive success represents the standard but often becomes logistically challenging, particularly for long-lived species where complete life cycles exceed experimental timeframes. Validated proxy fitness metrics offer practical alternatives when direct measurement becomes infeasible. Multi-year sampling enables estimation of both mean selection gradients and their temporal variance—both essential for dynamic $\boldsymbol{G}$-matrix forecasting models.

Allele-Based Forecasting: Population Genomic Sampling

Allele-based evolutionary forecasting requires population-scale genomic sampling that captures both standing genetic variation and its environmental associations over geographic and temporal scales. Minimum genomic sampling standards exceed those typically employed in population genetic surveys. Detecting environmental associations typically requires at least 20 unrelated individuals per population combined with sequencing depth ≥10× coverage to reliably distinguish genuine polymorphisms from technical artifacts (Nielsen et al. 2011). Geographic sampling design is important because environmental associations emerge from spatial correlations between allele frequencies and climatic gradients. Effective sampling requires population collections that span substantial environmental variation while maintaining sufficient geographic replication to distinguish genuine adaptive signals from population structure confounds. In practice, this typically demands sampling 10-20 populations in multiple environmental gradients with 20+ individuals per population. For instance, a study of 281 lodgepole pine populations by Mahony et al. (2020) exemplifies this approach. By sampling across extensive environmental gradients in western Canada (e.g., mean annual temperatures from -4°C to +9°C), they were able to identify climate-associated genetic variants. Crucially, their broad sampling was essential for distinguishing these adaptive signals from the confounding effects of the species' postglacial expansion, a historical factor that itself aligned with major environmental gradients. This work underscores the utility of large-scale genomic studies in providing data for climate-based seed transfer and conservation efforts.

Composite Adaptation Scores: Polygenic Architecture Integration

Composite adaptation score approaches integrate information from thousands of loci through weighted sums where each variant contributes according to its estimated effect size and current frequency. Statistical power requirements for polygenic score development exceed those for single-locus approaches substantially. Reliable effect size estimation typically requires genome-wide association studies with thousands of individuals to achieve adequate precision for variants explaining small phenotypic variance fractions. Multi-environment Genome Wide Association Studies (GWAS) are essential because effect sizes must generalize over environmental conditions where forecasts will be applied. Single-environment GWAS studies risk substantial bias when selection pressures differ between original study conditions and environments where predictions are needed (Table 3).

Cross-environment validation frameworks help tests of predictive accuracy while ensuring that genotype-environment relationships generalize beyond specific study conditions. For example, Exposito-Alonso et al. (2019) validated genomic predictions across 30 field sites spanning diverse European climates, demonstrating that composite adaptation approaches calibrated on contemporary populations could predict evolutionary responses to climate manipulation experiments. Implementation requires careful partitioning of available data into training and validation sets that maintain environmental independence while preserving adequate sample sizes for both effect size estimation and validation testing (Kawecki & Ebert 2004; Kawecki et al. 2012). Geographic stratification approaches that use distinct environmental regions for training versus validation can provide stringent tests of transferability. Temporal validation using historical samples provides additional evidence for polygenic score reliability by testing whether scores calibrated on contemporary populations can predict evolutionary changes observed in museum or herbarium specimens. These temporal tests reveal whether polygenic architectures remain sufficiently stable to enable forecasting in relevant timescales.

Integration strategies and adaptive management

The Mechanistic Foundation for Predictive Power

The predictive power of evolutionary forecasting emerges not from sophisticated statistical methods alone, but from mechanistic understanding of how environmental variation translates into fitness consequences through physiological processes. Traditional approaches that collapse climate complexity into annual averages fundamentally misrepresent the environmental variance that drives evolutionary responses, discarding precisely the information most relevant to management strategies. When micro-environmental loggers record temperature, humidity, and soil moisture at hourly intervals, they reveal selection-relevant patterns invisible to weather station averages—patterns that determine which genotypes survive extreme events and contribute to subsequent generations (Pettorelli et al. 2014; Fick & Hijmans, 2017).

This mechanistic perspective transforms how we interpret genotype-environment relationships. Rather than assuming linear correlations between climate variables and fitness, process-based environmental models enable direct linkage between environmental measurements and physiological outcomes. Energy balance models, for instance, predict how temperature and humidity combine to determine leaf temperatures and water loss rates under stress, while biogeochemical models reveal how soil chemistry modulates nutrient uptake during drought. These mechanistic insights provide the causal foundation that statistical associations alone cannot deliver.

Plasticity as the Bridge Between Genes and Environment

The relationship between genetic potential and realized evolutionary responses operates through phenotypic plasticity—the capacity for genotypes to express different phenotypes across environments (Lande 2009; Nicotra et al. 2010; Chevin et al. 2013; Ghalambor et al. 2015). This creates a fundamental interdependence: plasticity provides immediate population response to environmental change, determining which individuals survive and reproduce successfully enough to contribute genetic material to subsequent generations, thereby directly shaping the selection gradients that drive genetic evolution. Simultaneously, plastic responses buffer populations against environmental stress long enough for genetic adaptation to accumulate.

Understanding this interdependence requires measuring complete reaction norms—mathematical functions that precisely relate genotype, environment, and phenotype—rather than treating traits as static properties (Schlichting & Pigliucci, 1998; Des Marais et al. 2013). Common garden experiments that grow replicated genotypes across environmental gradients provide the empirical foundation for estimating these reaction norms. The resulting data reveal not just how traits respond to environment, but how genetic variation in plasticity itself shapes evolutionary trajectories.

Adaptive Management as Evolutionary Learning

The implementation of evolutionary forecasting demands a philosophical shift from prediction as endpoint to prediction as process. Adaptive management transforms forecasting from static exercise into dynamic, iterative learning that continuously improves accuracy by incorporating new information through targeted monitoring and experimental intervention (Walters, 1986; Williams, 2011). This approach treats initial evolutionary forecasts as working hypotheses rather than fixed predictions, deliberately designing near-term management actions to generate maximum information for improving subsequent iterations.

The practical implementation requires pre-specified "trigger points" where management actions activate regardless of remaining uncertainty, preventing analysis paralysis while maintaining flexibility for course corrections (Martin et al. 2009; Cook et al. 2016). When genetic diversity metrics drop below critical thresholds, assisted gene flow protocols activate automatically. When climate stress indices exceed predetermined tolerance limits, ex-situ conservation efforts begin immediately to preserve evolutionary potential while natural populations attempt in-situ adaptation (Aitken & Whitlock, 2013; Weeks et al. 2011; Havens et al. 2006). The aim shifts from perfect prediction to calibrated risk assessment that improves management decisions under uncertainty.

Digital Validation: Testing Predictions Before Implementation

Digital twin approaches provide the critical validation infrastructure for evolutionary forecasting by creating computational replicas of biological systems that can be tested against real-world outcomes before committing to costly interventions (Cooper et al. 2014; Haller & Messer 2019). These virtual populations, parameterized with empirical genetic and environmental data, enable researchers to test forecasting accuracy through controlled simulation experiments. Implementation involves creating population models that mirror real systems in genetic architecture, demographic parameters, and environmental responses (Technow et al. 2015).

As empirical data accumulate from monitored populations, digital twins undergo continuous updating and re-calibration, providing iterative improvement of forecasting accuracy (Hammer et al. 2019). Agricultural breeding programs demonstrate this approach by testing genomic selection strategies over multiple breeding cycles in silico, enabling optimization of selection intensities and population sizes before committing resources to long-term programs (Messina et al. 2011; Cooper et al. 2021). The same logic applies to conservation interventions—testing assisted gene flow or habitat management strategies virtually before implementing costly field programs (Flanagan et al. 2018; Razgour et al. 2019).

The integration of mechanistic understanding, plasticity dynamics, adaptive management, and digital validation creates a coherent framework for implementing evolutionary forecasting. Rather than viewing these as separate methodological additions, they represent interconnected components of a learning system that improves predictive capacity through systematic integration of biological understanding with empirical observation.

V. Conclusions—Evolution as Infrastructure

From theoretical possibility to operational reality

Evolutionary biology has achieved a transformation: the ability to forecast adaptive responses before they fully manifest in natural populations, though significant challenges remain in translating theoretical frameworks into reliable operational tools (Wortel et al. 2023). This capability emerged from recognizing that evolution shows scale-dependent predictability—outcomes are often more predictable than the mechanisms producing them—and that uncertainty can be treated as useful information rather than methodological failure. The three complementary approaches highlighted here—trait-based methods leveraging $\boldsymbol{G}$-matrix constraints, allele-based approaches tracking genomic mechanisms, and composite scores integrating polygenic architecture—now provide calibrated risk assessments over diverse biological systems and temporal scales. The practical demonstrations are compelling. Genomic vulnerability maps guide assisted migration of climate-threatened species (Fitzpatrick & Keller, 2015), agricultural breeding programs incorporate multi-generational climate projections into genomic selection strategies (Crossa et al. 2017), and forest managers deploy evolutionary predictions to inform reforestation spanning shifting climate envelopes. These applications demonstrate evolution's emergence as standard planning infrastructure alongside climate projections and demographic forecasts.

Integration across biological scales reveals predictable patterns

The success of evolutionary forecasting stems from matching analytical methods to biological scales where predictable patterns emerge from complex underlying processes. Rather than forcing uniform approaches onto different organizational levels, we exploit natural hierarchies of biological organization to extract maximum predictive information from available data. Trait-based approaches capture predictable phenotypic trajectories constrained by genetic architecture, providing reliable short-term forecasts when G-matrix relationships remain stable. Allele-based methods track mechanistic pathways through individual loci, offering medium-term predictions when environmental associations can be quantified reliably. Composite adaptation scores integrate distributed polygenic effects, enabling long-term projections under novel environmental conditions where neither trait-based nor single-locus approaches provide adequate signal. When multiple approaches are feasible, integration provides robust uncertainty quantification while revealing which biological scales drive predictable responses. An alpine plant study demonstrates this integration potential (Cotto et al. 2017): dynamic eco-evolutionary models combining demographic processes with genetic forecasting predicted that alpine species would persist longer than ecological niche models suggested but produce increasingly maladapted offspring—ideas that emerge only from cross-scale integration. Temporal validation spans systems from annual plants to viral evolution, suggesting that forecasting thinking is common across many distinct research fields. Resurrection ecology studies using stored seeds validate trait-based predictions during decades (Franks et al. 2007; 2016; Hamann et al. 2018. Time-series genomics tracks allele frequency predictions over seasons and years (Machado et al. 2021; Kelly, 2022). Composite adaptation scores demonstrate predictive accuracy for climate vulnerabilities decades into the future (Exposito-Alonso et al. 2019).

Constraints define reliable forecasting boundaries

Important limitations define where evolutionary forecasting remains unreliable. Prediction accuracy degrades for traits involving extensive epistatic interactions where individual locus effects depend strongly on genetic background. Demographic collapses can weaken genetic predictions when population bottlenecks eliminate the genetic variation that forecasting models assume remains available. Novel environmental conditions may trigger responses beyond current model capacity when environmental change exceeds the range of conditions used for parameter estimation (Jones et al. 2007; Melbourne & Hastings, 2008). Temporal horizons impose additional constraints that reflect fundamental evolutionary properties rather than temporary methodological shortcomings. Trait-based approaches prove most reliable for 5-20 generations when genetic architecture remains relatively stable. Allele-based methods extend to 20-100 generations but require environmental associations that may weaken as landscapes change. Composite scores become increasingly uncertain beyond 100 generations as polygenic architectures evolve and novel environmental conditions hinder effect size transferability. These limitations demand honest assessment of forecasting boundaries while identifying opportunities for improvement through better data collection, model development, and validation strategies. Rather than abandoning forecasting where uncertainty is high, we recommend quantifying that uncertainty explicitly to inform decision-making about when to act despite incomplete information versus when to collect additional data before intervening.

Adaptive management enables continuous improvement

The most promising implementations of predictive evolutionary genomics treat evolutionary forecasting as an iterative learning process rather than one-time prediction exercise. Adaptive management frameworks transform initial forecasts into working hypotheses that guide near-term interventions designed to generate maximum information for improving subsequent predictions (Walters, 1986; Williams, 2011). This approach acknowledges that initial forecasts will be imperfect while creating systematic pathways for improvement through targeted monitoring and experimental intervention. Rather than demanding impossible accuracy from initial limited datasets, adaptive management focuses on calibrated risk assessments that improve management decisions under uncertainty while building predictive capacity through systematic learning from forecast errors. Successful adaptive management requires pre-specified trigger points where conservation or management actions activate regardless of remaining uncertainty, preventing analysis paralysis while preserving flexibility for course corrections as new information becomes available.

Evolution is becoming predictable enough to serve as reliable infrastructure for evidence-based decision-making. The analytical frameworks exist, methodological approaches are empirically validated, and practical applications are scaling across multiple sectors. The central question is no longer whether we can predict evolutionary responses, but how wisely we will deploy this capability to safeguard the evolutionary processes that sustain life on Earth. The tools are ready, the need is urgent, and Earth's biological future depends on rapidly scaling evolutionary forecasting from research frontier to standard practice.

The responsibility is ours.

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Author Contributions

DO-B conceived the conceptual framework and wrote the first draft. All authors made intellectual contributions, made modifications and edited the paper.

Conflicts of Interest

We declare no conflicts of interest.

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Box 1: Temporal windows reflect detectability and parameter stability—not genetic architecture.

How genetic complexity determines prediction horizons through biological constraints

Short-, medium-, and long-term horizons are identifiability regimes set by selection, drift, sampling error, and the stability of model parameters. They are not statements about whether a trait is mono- or polygenic. Any architecture can be analysed on any horizon if the relevant quantities are estimable and kept in calibration. The bands we use are soft: roughly 5–20 generations when trait models retain calibration, ~20–100 generations when per-locus signals outpace noise, and 100+ generations when many weak effects dominate and aggregation becomes powerful.

Trait-based forecasts (≈5–20 generations).

Quantitative-genetic predictions exploit $\Delta\bar{z} \approx G\beta$ while $\boldsymbol{G}$ is locally stable and environmental covariance is controlled. Skill here hinges on parameter stability, replication, and design—not on whether the underlying architecture is mono- or polygenic. As selection, drift, mutation, or environment shift G, calibration erodes and forecasts degrade for that reason, not because "traits are polygenic". In practice, near-term responses in field or common-garden studies live in this window because G is estimable and behaves well over tens of generations.

Allele-based inference (≈20–100 generations).

Locus-specific trajectories become informative once per-locus selection s exceeds drift and sampling noise; the detection time scales on the order of $\sim 1/s$ given realistic sample sizes. Recombination, linkage, and demography set power, but architecture does not dictate the timescale: large-effect sweeps, moderate-effect haplotypes, or several loci with enough signal all qualify once trackable. This is the window where we can estimate s with tolerable error and follow alleles through time—think herbicide or pesticide resistance, or temperature-associated variants that move measurably across cohorts.

Composite (polygenic) scores (100+ generations).

As signals disperse across many loci and G drifts, aggregation gains power. Composite scores—polygenic predictors calibrated to observed fitness—summarise diffuse effects and support long-horizon projections. Their limiting factors are calibration and transfer: the mapping between predictors and fitness must hold under the environments to which we apply them, and extrapolation outside the training envelope must be flagged with uncertainty inflation. The virtue of this regime is not that it is "polygenic by definition", but that aggregation restores signal when per-locus effects are individually weak, and trait parameters no longer hold still.

Orthogonality. Time is not architecture. The ≈5–20, 20–100, and 100+ generation bands describe detectability and parameter stability. We should choose methods by what is identifiable and calibratable for the question at hand—in other words, use trait models when G is stable, allele trajectories when s clears noise, and composite scores when signals are diffuse and horizons are long.

Notation: $\bar{z}$, mean trait vector; G, additive genetic (co)variance; β, directional selection gradient; s, per-locus selection; "composite score", a calibrated polygenic predictor of fitness or trait under environment E.

Box 2: *Arabidopsis* Climate Adaptation Case Study

Empirical Demonstration of Evolutionary Forecasting

This case study summarises a globally synchronised, multi-year evolution experiment in *Arabidopsis thaliana* that measured rapid adaptation and extinction risk across climates. Over five years and more than thirty outdoor gardens spanning Europe, the Levant, and North America, the team sequenced ~70,000 surviving reproductive individuals, directly observing repeatable, climate-linked genetic change and population outcomes.

We treat fitness as the prediction target. Trait information enters through estimated selection gradients β; allele information enters through locus-specific selection coefficients s; genome-wide signals enter through a calibrated polygenic predictor of fitness (a composite score). The model links genotype and environment to observed fitness with a hierarchical likelihood, expresses forecasts as $p\{w(t) \mid E(t)\}$, and reports uncertainty from parameters, demography, and climate scenarios. In this framing, "genomic offset" functions as a polygenic fitness score once trained on observed www.

Short horizon. Skill is assessed on held-out gardens, years, or accessions within $\leq$ five generations using proper scoring rules (e.g., log score) and error on fitness (RMSE), with credible intervals. Highest skill is expected when forecast climates lie inside the training envelope, with quantified decay as climates diverge.

Medium horizon. When per-locus signals clear drift and sampling noise, allele trajectories provide estimates of s and enable locus-level forecasts; detection time scales on the order of $1/s$ given realistic sampling. Power hinges on recombination, LD, and demography inferred from the same data.

Long horizon. As signals disperse across many loci and G drifts, aggregation gains power. Composite scores, calibrated to fitness in the gardens, support decadal projections (e.g., 2050/2070) with transfer checks and uncertainty inflation outside the training envelope. The posterior $p\{w(t)\}$ naturally integrates β, s, and composite effects, producing unified fitness forecasts under explicit $E(t)$.

Limits. Forecasts remain contingent on calibration and environmental coverage. Population structure, $\boldsymbol{G \times E}$, and plasticity are modelled where estimable; where not, we state the limits on external validity. The approach is general, but the *Arabidopsis* experiment provides rare, direct evidence that links replicated climate exposure, genome-wide change, and realised fitness over multiple years and sites.

Attribution note: Case study adapted from Exposito-Alonso and collaborators' preprint on synchronised outdoor evolution gardens in *A. thaliana* (Wu et al. 2025).

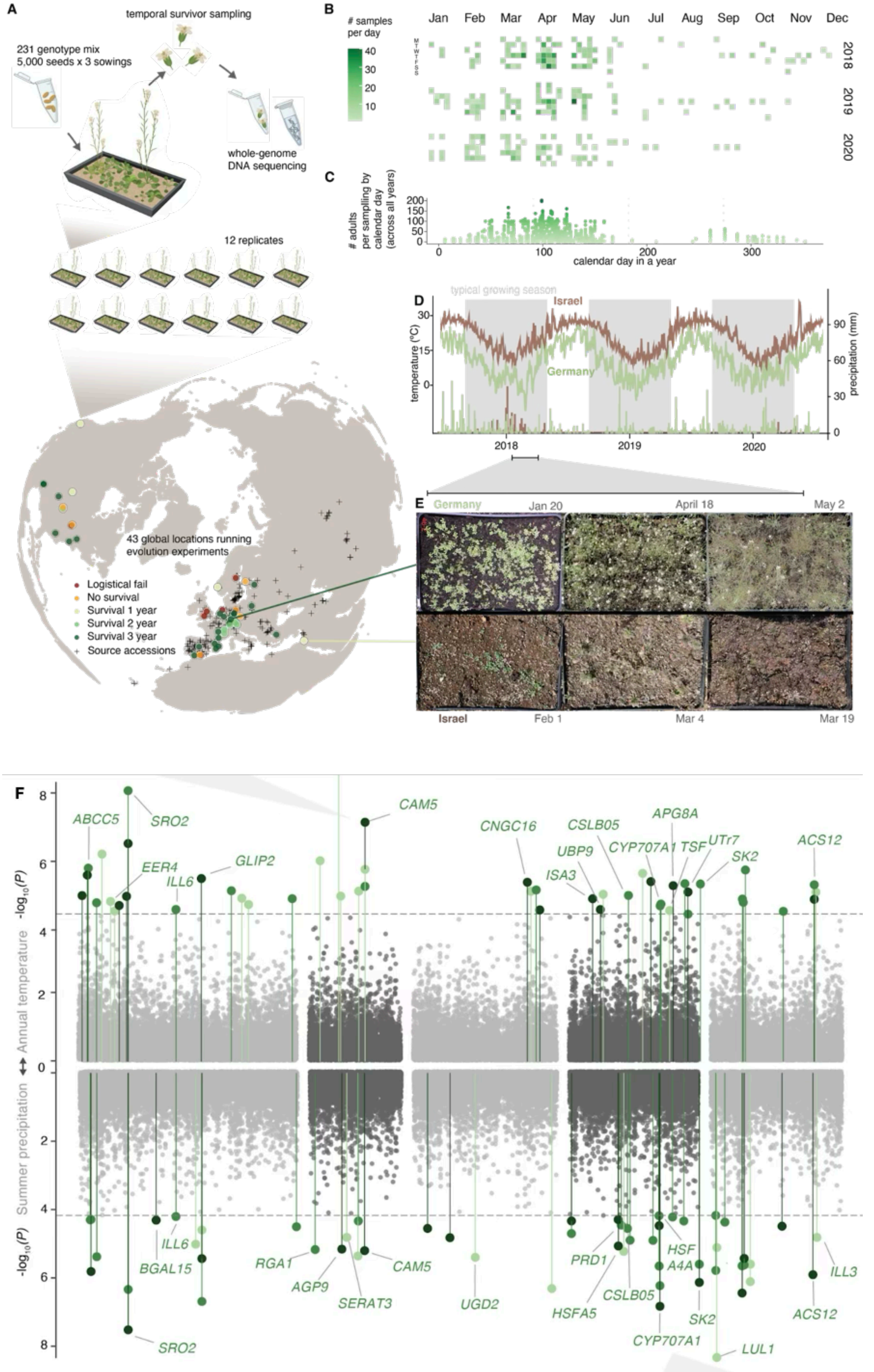

A
temporal survivor sampling
231 genotype mix
5,000 seeds x 3 sowings
whole-genome DNA sequencing
12 replicates
43 global locations running evolution experiments
Logistical fail
No survival
Survival 1 year
Survival 2 year
Survival 3 year
Source accessions
B
samples per day
40
30
20
10
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec
2018
2019
2020
C
adults per sampling by calendar day (across all years)
calendar day in a year
D
typical growing season
Israel
Germany
temperature (°C)
precipitation (mm)
2018
2019
2020
E
Germany Jan 20 April 18 May 2
Israel Feb 1 Mar 4 Mar 19
F
-log10(P)
Annual temperature
Summer precipitation
ABCC5
SRO2
EER4
ILL6
GLIP2
CAM5
CNGC16
CSLB05
APG8A
UBP9
CYP707A1
TSF
UTr7
ISA3
SK2
ACS12
BGAL15
RGA1
AGP9
SERAT3
UGD2
HSFA5
PRD1
HSF A4A
LUL1
ILL3

Figure B2. GrENE-net's globally distributed evolution experiment in *Arabidopsis thaliana* and genome–environment signals. **A** Experimental design. 231 accessions mixed in tubes of ~5,000 seeds; each tray was sown with three tubes, with sowing every two weeks through autumn 2017 to ensure establishment. Each site started 12 trays as independent replicates. The map shows 43 gardens (sites); colours indicate outcomes, with 30 sites completing at least one generation and producing genomic data. **B** Calendar of time-series flower-tissue collections used for genomic sequencing during the first three years. **C** Density of samples collected across the calendar year, pooling all three years. **D** Daily temperature curves and precipitation bars over the first three years at two example locations: humid continental Würzburg, Germany (site #46, green) and arid desert Sde Boker, Negev, Israel (site #26, brown). **E** Example photographs of experimental populations in Germany and Israel during spring of the first growing season (dates as labelled). **F** Experimental-evolution Genome–Environment Associations (eGEA) with temperature and summer precipitation. Manhattan-style summary combining LFMM, quasi-binomial GLMM, and Kendall correlation, with haplotype-block P-value pooling by WZA. Top: associations with mean annual temperature; bottom: associations with summer precipitation. Y-axis is $-\log_{10}(P)$; the five chromosomes are shown in alternating grey/black; selected candidate genes are annotated. *Panels (a–e) adapted from Fig. 1 and panel (f) from Fig. 4D of Exposito-Alonso et al., bioRxiv 2025 (doi:10.1101/2025.05.28.654549).*

Figure Legends

Figure 1. Historical development of theoretical foundations enabling predictive evolutionary genomics

The timeline traces conceptual advances from early mathematical foundations through the convergence of distinct theoretical streams into modern predictive frameworks. The quantitative genetics tradition developed from Lush's breeder's equation through Fisher's infinitesimal model to Lande's multivariate $\boldsymbol{G}$-matrix framework, emphasizes trait-based approaches to evolutionary prediction. The population genetics tradition evolved from Hardy-Weinberg equilibrium through the foundational work of Fisher, Wright, and Haldane on allele frequency dynamics, extending through Kimura's diffusion theory to modern coalescent approaches. The integration phase (1980s-1990s) unified these traditions into coherent evolutionary theory, while the genomics era enabled practical implementation through Bayesian methods, genomic selection, and population genomics approaches (GWAS, GEA, ancient DNA). The modern synthesis combines these elements into the contemporary framework enabling probabilistic evolutionary forecasting with explicit uncertainty quantification. Color progression marks the historical transition from foundational theory through classical development, integration, and modern applications to current predictive capabilities.

Figure 2. Empirical windows for evolutionary forecasts across genetic architecture, space and time. The isometric cube locates three forecasting approaches in a shared three-dimensional space defined by genetic architecture (few → many loci, vertical axis), spatial scale (single → many populations, front axis) and temporal scale in generations (near → far future, right axis). Semi-transparent slices show where each approach is most reliable: a purple plane marks trait-based models that work for roughly 5–20 generations while the ancestral $\boldsymbol{G}$-matrix remains stable; a red plane marks allele-based inference that becomes informative over about 20–100 generations once selection can outrun drift at individual loci; and a green plane marks polygenic or composite scores that dominate beyond 100 generations when many loci and traits contribute to adaptation and the $\boldsymbol{G}$-matrix has shifted. Grey spheres place representative study systems on each slice, while a blue fan of arrows sketches probable evolutionary trajectories as selection, drift and contingency reshape genetic architecture through time—from short-term trait responses based on standing variation, through selective sweeps or concurrent allele shifts, to long-horizon polygenic change (**Box 1**). These detectability surfaces arise from biological and sampling limits rather than methodological preference and provide the scaffold for the Bayesian integration framework developed in the main text and **Figure 3**.

Figure 3. Modular Bayesian workflow for evolutionary forecasting

The probabilistic integration framework combines five information streams to generate actionable evolutionary forecasts. Theoretical priors encode accumulated evolutionary understanding from decades of quantitative genetic research, population genetic theory, and meta-analyses of demographic parameters. Fitness data from field measurements of reproductive success quantify selection gradients operating on multiple traits simultaneously. Environmental data capture climate patterns, soil chemistry, and disturbance regimes at scales relevant to selection pressures. Phenotypic data from multivariate trait measurements enable estimation of genetic variance-covariance matrices and constraint structures. Genomic data including allele frequencies and variant effects provide the raw material for evolutionary responses. These streams feed into a probabilistic integration engine where Bayesian algorithms (MCMC, ABC, or Variational Bayes) combine empirical evidence with theoretical understanding: $P(\theta|Data) \propto P(Data|\theta) \cdot P(\theta)$. The framework outputs probabilistic forecasts as full posterior distributions with credible intervals and quantified uncertainty, enabling evidence-based conservation and management decisions while treating uncertainty as valuable information rather than methodological limitation.

Table 1. Evolutionary Prediction Studies: Key Systems and Temporal Scales

GEA = Genotype-Environment Association; GDM = Generalized Dissimilarity Modeling; GWAS = Genome-Wide Association Study. Study types distinguish retrodictive validation using historical data from predictive forward-looking forecasts. Forecasting Approach classifications follow the three-scale framework: Trait-Based (5-20 generations, $\boldsymbol{G}$-matrix constraints), Allele-Based (20-100 generations, individual loci tracking), Composite Adaptation Score (50-100+ generations, polygenic integration), Multi-Approach (combining methods), and Specialized (system-specific methods). Examples emphasize plant systems while demonstrating broad taxonomic applicability of evolutionary forecasting approaches.

Study System	Study Type	Prediction Focus	Timeframe	Analytical Approach	Forecasting Approach	Key Results	Validation Strategy	References
Arabidopsis thaliana	Predictive	Climate adaptation and survival under warming	30 years (2050 projections)	GWAS integrated with GEA and random forest modelling	**Composite Adaptation Score**	Identified 7-89 causal loci under natural selection by climate variables; generated population-specific vulnerability assessments	Common garden validation under simulated future climates; historical selection signature analysis	Exposito-Alonso et al. (2019)
Arabidopsis thaliana	Predictive	Extreme drought adaptation potential	~50 years (2070 projections)	Controlled drought experiments with predictive modelling	**Composite Adaptation Score**	Central European populations predicted to show adaptation lag under 21st century climate scenarios	Terminal drought stress validation experiments	Exposito-Alonso et al. (2018)

Brassica rapa	Retrodictive	Flowering phenology and drought response evolution	7 generations	Resurrection ecology with genome sequencing	**Trait-Based**	Rapid evolution toward earlier flowering under drought stress; detected divergent short-term versus long-term selection signatures	Ancestral-descendant seed comparisons among controlled environments	Franks et al. (2007, 2016)
Brassica rapa	Retrodictive	Multi-decadal evolutionary responses	20 years	Resurrection ecology integrated with long-term field monitoring	**Trait-Based**	Documented evolutionary responses to precipitation fluctuations; suggested evolutionary rates may lag environmental change	Stored seed resurrection experiments spanning two decades	Hamann et al. (2018)
Populus balsamifera	Predictive	Climate adaptation through genomic offset analysis	~40 years (2050 projections)	Genomic offset modeling using gradient forests and GDM	**Composite Adaptation Score**	Northwestern populations identified as most climatically vulnerable; developed robust gradient forest framework	Comparative genomic offset approach validation	Fitzpatrick & Keller (2015)
Four perennial alpine species	Predictive	Range shifts under climate warming	~180 years (1970-2150)	Dynamic eco-evolutionary modeling with demographic integration	**Multi-Approach** (Trait + Composite)	Alpine plants predicted to persist longer than niche models suggest but produce increasingly maladapted offspring	Demographic simulations integrated with genetic forecasting models	Cotto et al. (2017)
Mimulus guttatus	Retrodictive	Genome-wide fluctuating selection patterns	23 generations	Time-series genomics with selection analysis	**Allele-Based**	Documented temporally variable selection from 1.86 million SNPs with high variance in selection	Long-term field monitoring combined with	Kelly (2022)

						intensity	genome-wide analysis	
Drosophila melanogaster	Predictive	Seasonal adaptation and allele frequency cycling	6 months	Temporal genomics with generalized linear modeling	**Allele-Based**	High predictability in most populations; environmental extremes reduce forecast accuracy	Leave-one-out cross-validation during seasonal cycles	Machado et al. (2021)
Escherichia coli	Retrodictive	Beneficial mutation proportion during long-term evolution	50,000 generations	Experimental evolution with genome sequencing	**Allele-Based**	Most fixed mutations proved beneficial rather than neutral, contradicting neutral theory expectations	Comparison with mutation-accumulation experiment controls	Tenaillon et al. (2016)
***Influenza* A virus**	Predictive	Clade frequency dynamics and antigenic evolution	1 year	Fitness modeling integrated with epidemiological dynamics	**Specialized Viral** (Non-standard)	Achieved up to 93% prediction accuracy for dominant lineages; revealed strain-specific fitness variation	Retrospective validation against global surveillance data	Łuksza & Lässig (2014)
Helianthus annuus x H. debilis	Predictive	Effect of hybridization on repeatability of evolution	13 years	Time-series genomics with selection analysis	**Allele-Based**	Evolution was highly parallel throughout replicates, with shared selection driving 88% of variance in introgressed allele frequency change	Long-term field monitoring combined with genome-wide analysis. Common garden validation	Mitchell et al. (2022); Owens et al. (2025)

Table 2. Data Architecture for Evolutionary Forecasting

Essential data requirements span seven hierarchical layers from genomic foundations through adaptive management infrastructure, with implementation guidelines tailored to specific forecasting approaches. Genomic data provides the raw material for evolutionary responses and drives likelihood functions linking environmental gradients to genetic changes. Field phenotypes and fitness measurements anchor empirical estimates of selection gradients and validate evolutionary predictions. Environmental characterization captures selection pressures operating at relevant scales, while temporal baselines establish starting points for evolutionary forecasts and detect population demographic changes. Regulatory and multi-omic extensions capture heritable variation invisible to DNA sequence analysis alone. Adaptive management infrastructure enables continuous forecast improvement through systematic learning from prediction errors. Priority levels indicate relative importance for each forecasting approach: Essential (required for reliable predictions), High (substantially improves accuracy), Moderate (beneficial when resources permit), Low (optional enhancement).

Data Layer	Variables	Implementation Guidelines	Forecasting Approach Priority	Critical for Uncertainty Quantification
Genomic Foundation	Genome-wide variant discovery with adequate coverage and population sampling to distinguish genuine polymorphisms from technical artifacts. Capture structural variants and haplotype information when feasible. Gene expression data from relevant tissues and developmental stages.	Deploy reference assemblies to anchor variant identification. Implement balanced sampling spanning geographic sites and temporal periods to distinguish spatial from evolutionary signals.	**Essential**: Allele-Based, Composite **Moderate**: Trait-Based	Allele frequency data drives likelihood functions linking environmental gradients to genetic changes. Expression data identifies plastic responses that may confound or mediate adaptive evolution.
Regulatory and Multi-omic Extensions	Heritable regulatory variation including DNA modifications, chromatin structure, and post-translational regulation.	Sample representative subsets of genomically-characterized individuals to balance costs with coverage. Process treatment and control conditions in parallel to capture regulatory responses.	**High**: Composite **Moderate**: Allele-Based **Low**: Trait-Based	Captures heritable variation invisible to DNA sequence analysis alone. Provides empirical estimates for unexplained heritability components in forecasting models.
Field Phenotypes	Core life-history traits: survival, reproductive output, phenological timing. Functional traits relevant to environmental stress and adaptation. Scale: hundreds of	Implement systematic tracking with standardized measurement protocols. Integrate automated remote sensing with ground-based validation	**Essential**: Trait-Based **High**: Composite	Phenotypic distributions provide empirical anchors for selection gradient estimation while validating evolutionary predictions. Multi-year

	individuals per site over multiple years and environmental conditions.	measurements using consistent spatial sampling.	**Moderate**: Allele-Based	data enables separation of plastic versus genetic responses.
Environmental Characterization	Microclimate: high-resolution temperature, humidity, and moisture logging. Soil properties: chemistry, texture, and nutrient status over relevant spatial scales. Macroclimate: gridded environmental data. Disturbance history: anthropogenic and natural perturbation records.	Co-locate environmental monitoring with genetic sampling locations. Implement systematic calibration and maintain physical archives for future reanalysis.	**Essential**: All approaches	Drives likelihood functions connecting environmental gradients to fitness outcomes through mechanistic understanding of selection pressures operating at relevant scales.
Temporal Baselines	Historical biological materials spanning multi-decadal periods; long-term environmental records from multiple sources.	Utilize available biological archives under controlled revival conditions to measure traits. Apply appropriate molecular techniques for temporal genetic analysis.	**High**: Trait-Based (resurrection ecology) **Moderate**: Allele-Based, Composite	Establishes temporal starting points for evolutionary forecasts while detecting population demographic changes that could confound evolutionary inference.
Fitness Quantification	Absolute fitness through lifetime reproductive success; relative fitness through comparative performance measures. When direct measurement is impractical, employ validated proxy metrics combining survival and reproductive components.	Implement sampling strategies that balance measurement intensity with population coverage, maintaining validation subsets for direct fitness measurement.	**Essential**: All approaches	Transforms phenotypic changes into selection gradient estimates, completing the empirical chain linking environmental change through genetic architecture to evolutionary outcomes.
Adaptive Management Infrastructure	Standardized monitoring protocols; trigger points for intervention; decision frameworks; stakeholder	Establish clear protocols for model updating as new data become available. Pre-specify intervention thresholds to prevent analysis paralysis. Maintain long-term data	**Essential**: All approaches (implementation)	Enables continuous forecast improvement through systematic learning from prediction errors. Provides framework for evidence-

	communication systems; iterative model updating procedures.	continuity through personnel and institutional changes.		based decision making under uncertainty.

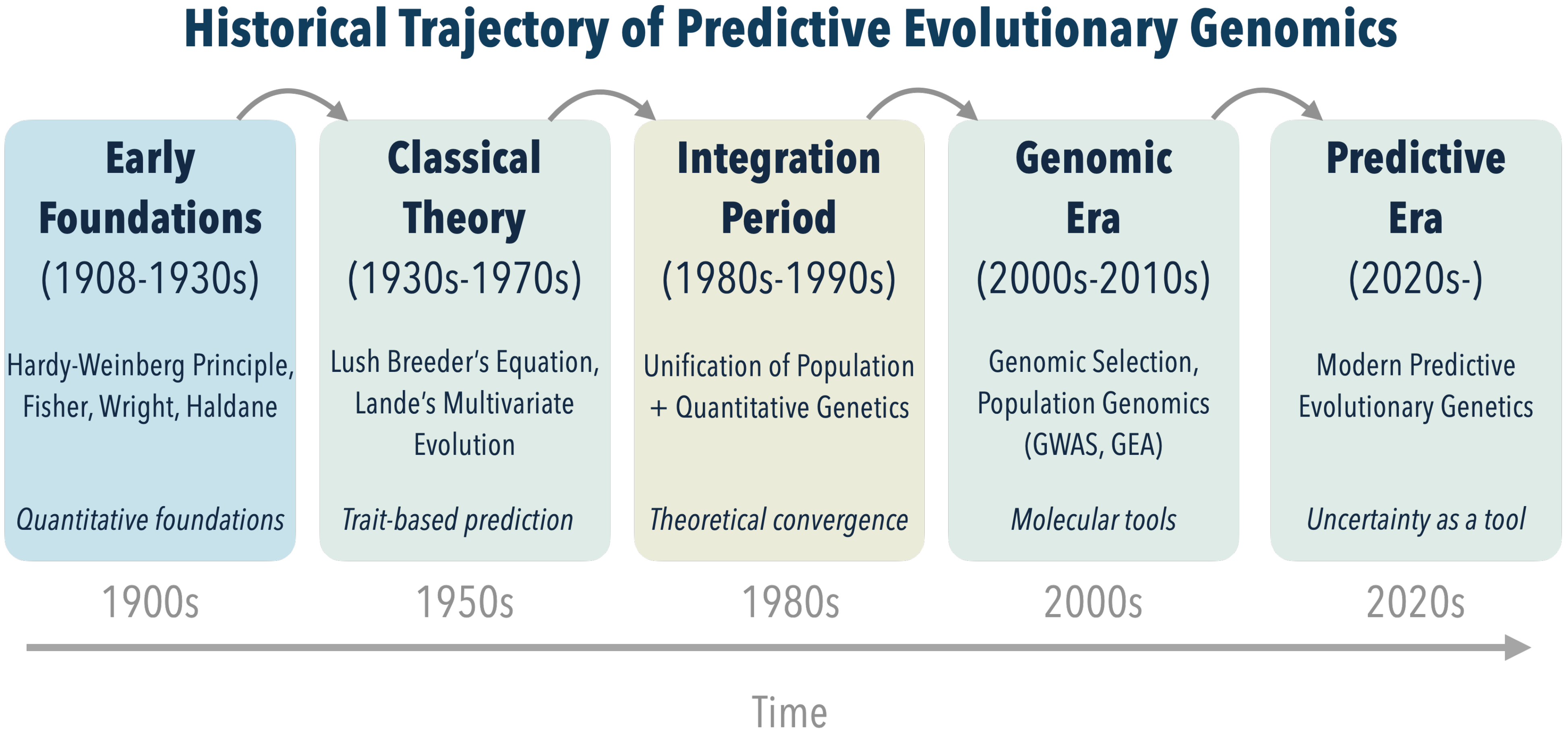
Table 3: Key Consideration and Potential Pitfalls in Evolutionary Forecasting.

Successful evolutionary forecasting requires systematic validation against independent temporal or spatial data whenever possible, embracing uncertainty by reporting credible intervals and validating model calibration rather than seeking false precision. Methods should match biological scales, using trait-based approaches for short-term predictions with simple architectures and composite scores for long-term polygenic traits. Throughout implementation, researchers must monitor whether G-matrices, selection coefficients, and environmental relationships remain stable over prediction horizons.

Category	Specific Issue	Consequence	Detection/Prevention
Data Quality	Insufficient sequencing depth (<10×) or population sampling (<20 individuals)	False polymorphisms inflate evolutionary signal; rare beneficial alleles missed	Verify call quality metrics; increase sampling; validate subset with deep sequencing
	Population structure confounding environmental associations	Spurious adaptive signals from shared ancestry rather than selection	Include kinship matrices or PCs in models; test geographic vs. environmental predictors
	Temporal sampling misalignment	Genetic changes attributed to wrong environmental drivers	Synchronize genetic sampling with environmental measurements; account for generation time
Model Assumptions	Static $\boldsymbol{G}$-matrix assumption in trait-based approaches	Systematic forecast degradation over extended timescales	Monitor $\boldsymbol{G}$-matrix stability across environments; use dynamic models for >20 generations
	Additive genetic effects assumption in composite scores	Underestimate responses when epistasis is strong	Test for interaction effects; compare additive vs. non-additive models
	Constant selection coefficients over time	Poor transferability to novel environmental conditions	Validate across multiple environments; model GxE interactions explicitly
Environmental Bias	Single-environment GWAS for multi-environment predictions	Effect sizes don't generalize; systematic prediction bias	Conduct multi-environment GWAS; validate across contrasting conditions
	Weather station vs. microclimate mismatch	Missing selection-relevant environmental variation	Deploy local sensors; validate remote sensing with ground truth
	Novel climate conditions beyond calibration range	Model extrapolation failure; unpredictable responses	Test model performance at environmental extremes; acknowledge uncertainty bounds

Temporal Validity	Rapid genetic architecture evolution	$\boldsymbol{G}$-matrix becomes outdated; constraint predictions fail	Update $\boldsymbol{G}$-estimates regularly; use shorter prediction horizons
	Demographic catastrophes override genetic predictions	Population crashes eliminate genetic variation faster than selection can act	Monitor effective population size; include demographic stochasticity in models
	Historical baseline bias	Cryptic population turnover confounds evolutionary inference	Verify population continuity; use multiple temporal samples
Statistical Power	Insufficient replication for $\boldsymbol{G}$-matrix estimation	Imprecise off-diagonal elements; unreliable constraint predictions	Minimum 100 genotypes × 3 environments; focus on major traits
	Weak environmental associations for allele-based approaches	Poor selection coefficient estimates; low prediction accuracy	Sample across broader environmental gradients; increase population number
	Small effect sizes in polygenic traits	Individual variants undetectable; composite scores unreliable	Use larger GWAS sample sizes (>5,000 individuals); focus on major-effect loci
Interpretation Errors	Confusing prediction accuracy with biological certainty	Overconfident management decisions despite inherent uncertainty	Always report credible intervals; validate against independent data
	Assuming linear responses to environmental change	Missing threshold effects and tipping points	Test for nonlinear relationships; model multiple scenarios
	Ignoring plasticity-evolution interactions	Underestimate total adaptive capacity; miss buffering effects	Measure reaction norms; integrate plastic and genetic responses

Figure 1


Historical Trajectory of Predictive Evolutionary Genomics
Early Foundations (1908-1930s)
Hardy-Weinberg Principle, Fisher, Wright, Haldane
Quantitative foundations
Classical Theory (1930s-1970s)
Lush Breeder's Equation, Lande's Multivariate Evolution
Trait-based prediction
Integration Period (1980s-1990s)
Unification of Population + Quantitative Genetics
Theoretical convergence
Genomic Era (2000s-2010s)
Genomic Selection, Population Genomics (GWAS, GEA)
Molecular tools
Predictive Era (2020s-)
Modern Predictive Evolutionary Genetics
Uncertainty as a tool
1900s
1950s
1980s
2000s
2020s
Time

1028 **Figure 2**

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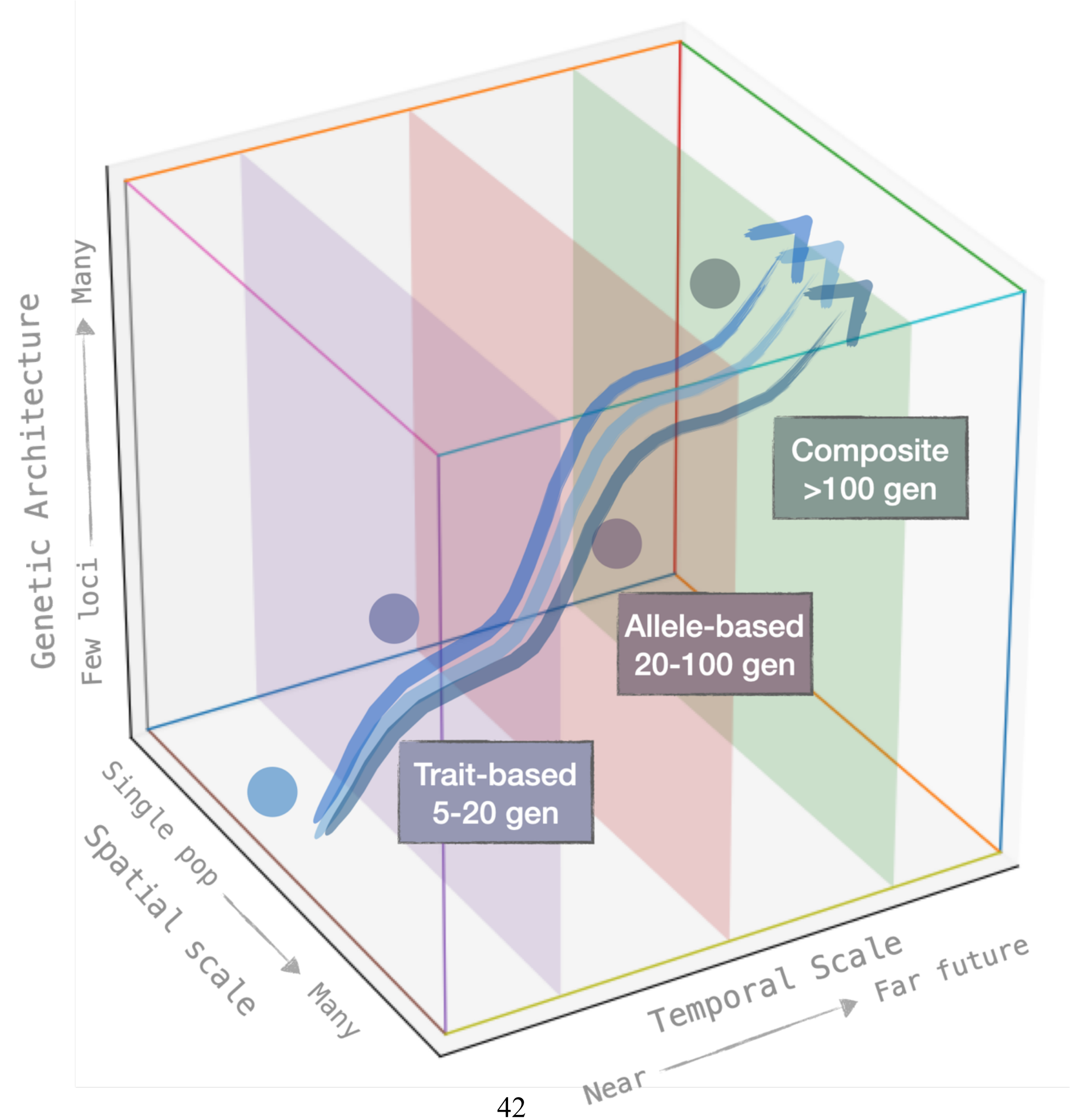
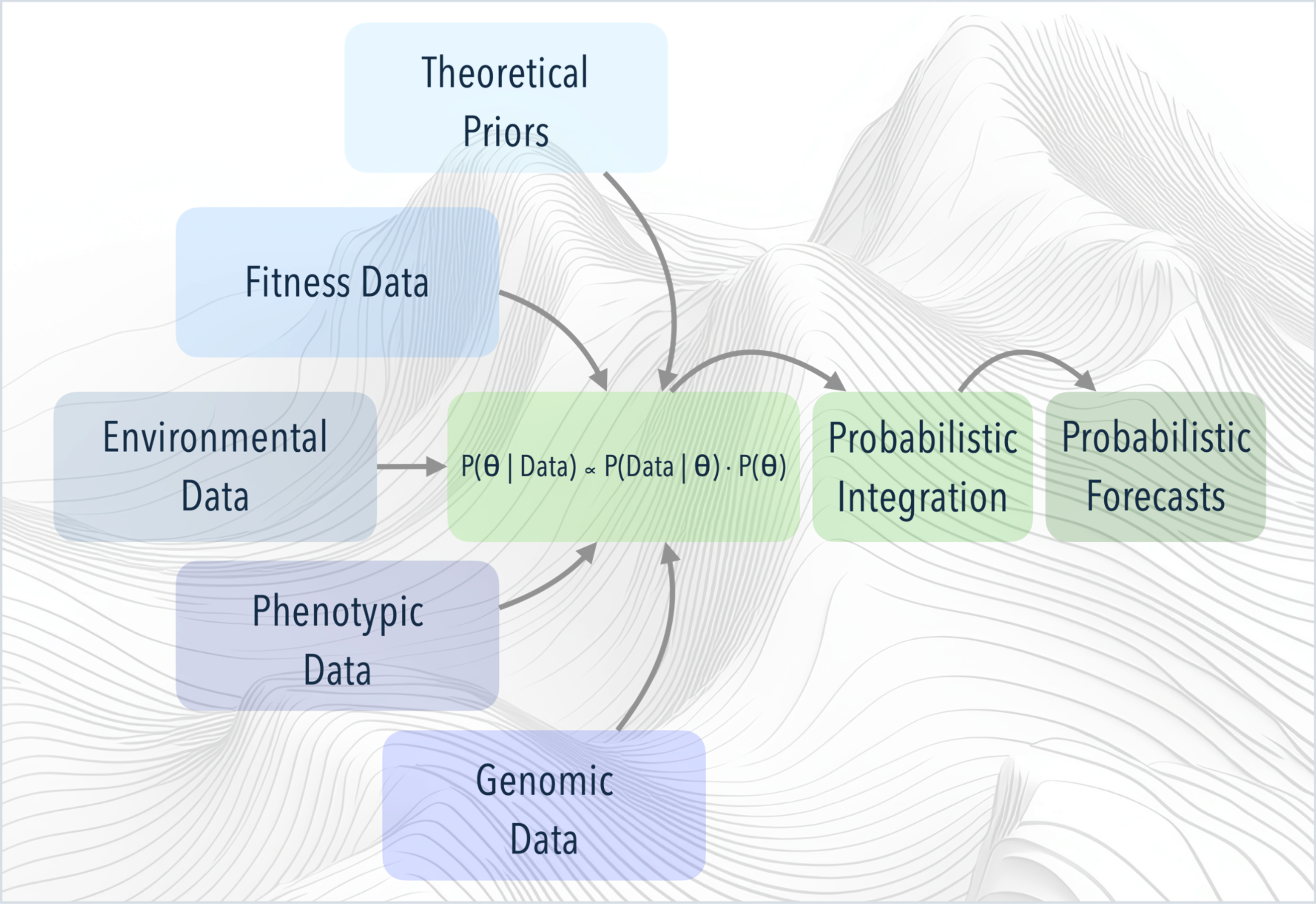


Figure 3


Theoretical Priors
Fitness Data
Environmental Data
$P(\theta \mid Data) \propto P(Data \mid \theta) \cdot P(\theta)$
Probabilistic Integration
Probabilistic Forecasts
Phenotypic Data
Genomic Data

Supplementary Table 1. Analytical Frameworks for Predictive Evolutionary Genomics

Approach	Core Methodologies	Primary Strengths	Key Limitations	Optimal Applications
Mechanistic Models	Lande's multivariate equation for trait evolution (Lande, 1979); individual-based population models (Haller & Messer, 2019); reaction-diffusion frameworks for spatial dynamics (Barton & Turelli, 1989); stochastic differential equations capturing demographic noise (Wright, 1932; Kimura, 1964)	Provide biologically interpretable predictions by exposing causal mechanisms underlying evolutionary change. Function effectively with limited empirical data while building on established evolutionary theory foundations that enable transparent scientific communication.	May oversimplify complex genetic architectures involving extensive epistasis. Become computationally intensive for scenarios with complex demographic structure and require explicit specification of all evolutionary parameters.	Short-term forecasts spanning fewer than 20 generations; systems with well-characterized genetic architecture; conservation planning applications requiring transparent, interpretable logic for stakeholder communication.
Machine Learning	Deep neural networks for pattern recognition (LeCun et al. 2015); ensemble methods including random forests and gradient boosting (Rellstab et al. 2015); Approximate Bayesian Computation for intractable likelihoods (Csilléry et al. 2010); forward population genetic simulators like SLiM (Haller & Messer, 2019)	Excel at detecting non-linear relationships in high-dimensional genomic data while capturing complex genotype-by-environment interactions without requiring explicit mathematical specification of underlying biological relationships.	Suffer from limited interpretability that obscures biological understanding ("black box" problem). Risk overfitting to training data and may learn spurious correlations that fail to generalize, while requiring training datasets for reliable parameter estimation.	Complex polygenic traits showing extensive epistatic interactions; high-dimensional genomic datasets; rapidly changing selection landscapes where traditional methods may fail to capture nonlinear relationships (Łuksza & Lässig, 2014); automated pattern detection in environmental genomics applications (Rellstab et al. 2015); viral evolution prediction (Hayati et al. 2020).
Hybrid Approaches	Theory-guided machine learning frameworks that integrate mechanistic biological understanding with computational prediction (Cooper et al. 2021); neural networks incorporating biological kernels; Bayesian model averaging over multiple analytical paradigms (Gelman et al. 2013); cross-species parameter inference through comparative genomic approaches (Rellstab et al. 2015)	Successfully balance biological interpretability with analytical flexibility by incorporating established evolutionary constraints while leveraging machine learning's pattern detection capabilities. Quantify model uncertainty through principled integration of multiple analytical approaches.	Involve increased implementation complexity requiring expertise in computational and biological domains. Present parameter tuning challenges while demanding computational resources for ensemble approaches.	Long-term predictions exceeding 20 generations; multi-omics data integration requiring synthesis from several biological scales (Hasin et al. 2017); agricultural breeding programs balancing multiple objectives (Cooper et al. 2021); conservation risk assessment demanding rigorous uncertainty quantification.

Supplementary Table 2. Evaluation Metrics for Evolutionary Forecasting Performance

Metric Category	**Specific Measures**	**Methodological Description**	**Primary Applications**
Point Forecast Accuracy	Root Mean Square Error (RMSE); Mean Absolute Error (MAE)	Quantify average prediction error magnitude by comparing point estimates (posterior means or medians) against observed evolutionary outcomes. Lower values indicate superior forecasting accuracy from continuous trait distributions.	Assessing prediction quality for quantitative traits including phenotypic evolution, allele frequency changes, and fitness component responses under environmental stress.
Explanatory Power	Coefficient of Determination (R^2)	Measures the proportion of empirical variance in evolutionary outcomes explained by model predictions. Values approaching unity indicate strong explanatory fit, while low values suggest inadequate model specification or excessive stochasticity.	Evaluating overall model performance for continuous evolutionary responses while identifying systems where prediction may be limited by stochastic processes.
Probabilistic Calibration	Reliability diagrams (calibration plots)	Provide visual assessment of forecast calibration by comparing predicted probability distributions against observed outcome frequencies. Well-calibrated models show diagonal relationships where stated confidence levels match empirical coverage rates.	Validating Bayesian forecasting frameworks where uncertainty quantification is important for evidence-based conservation and management decisions requiring risk assessment.
Integrated Forecast Quality	Proper scoring rules including Brier Score and Log Score	Simultaneously evaluate both prediction accuracy and calibration quality by rewarding forecasts assigning high probability to observed outcomes while penalizing overconfident or poorly calibrated predictions.	Probabilistic forecast evaluation enabling comparison of different modeling approaches while identifying optimal forecasting strategies for specific biological systems.
Classification Performance	Area Under the Receiver Operating Characteristic Curve (AUC)	Measures discriminatory ability for categorical evolutionary outcomes including adaptation versus maladaptation, population persistence versus extinction, or successful versus failed conservation interventions. Values near 0.5 indicate random performance while unity represents perfect classification.	Evaluating conservation triage applications where populations must be classified by risk level, or breeding programs requiring selection of genotypes most likely to succeed under projected environmental conditions.
Uncertainty Communication	Confidence and Credible Intervals	Provide probabilistic ranges expected to contain true evolutionary outcomes with specified probabilities. Interval width directly reflects prediction uncertainty, enabling transparent communication of forecasting limitations to stakeholders and decision-makers.	Supporting evidence-based management decisions by communicating prediction uncertainty transparently while enabling robust conservation strategies that acknowledge forecasting limitations inherent in complex evolutionary systems.