Genomic perspectives on the inference of evolutionary changes in ecological life-history traits

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Abstract

Genome-wide polymorphism data are increasingly used in conservation biology, and new developments in theoretical population genomics generate refined statistical inference methods. However, most theories and methods remain based on human life-history traits and genome characteristics, namely that the ratio of the population rates of recombination over mutation is approximately one. However, most fungal, invertebrate or plant species exhibit violations of the classic population genetics models due to their peculiar life cycles, such as long-life span and generation overlap, dormancy, clonality, selfing, and large variance in offspring production (sweepstakes reproduction). We first present applicable inference methods accounting for these life-history traits. Second, we highlight new inference methods to estimate the timing and magnitude of changes in these traits over evolutionary times. We suggest that methodological and theoretical novelties pave the way to dissect the causes and consequences of changes in ecological and evolutionary (life-history) traits in plant species and in multi-species assemblages (communities) in response to changing environments.

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1 Introduction: *The known knowns*

1.1 The age of population genomics

With technological advances, recent projects aim to build reference genomes for all pro- and eukaryotic species on Earth, including global initiatives such as the Earth BioGenome Project and regional efforts such as the Darwin Tree of Life Project (Darwin Tree of Life Project Consortium et al., 2022; Lewin et al., 2022). Consequently, population genomics based on reference genomes and population polymorphism data is, and will increasingly be, used as a major tool to inform conservation biology from populations up to ecosystem levels (Darwin Tree of Life Project Consortium et al., 2022; Formenti et al., 2022; Hohenlohe et al., 2021; Lewin et al., 2022; Theissinger et al., 2023). Conservation genomics as a predictive science aims to 1) quantify the available neutral and selective genetic diversity of species (Waldvogel et al., 2020), 2) link this diversity to the past and current geographic range of species(Aitken et al., 2024; Benestan et al., 2016), 3) assess the impact of future changes in species range, landscape and habitats on genetic diversity (Hohenlohe et al., 2021; Theissinger et al., 2023), and 4) anticipate the future adaptive potential of species (Aitken et al., 2024; Theissinger et al., 2023). More specifically, this research program attempts to quantify the genome-wide effects of demographic events (bottlenecks), spatial structuring and gene flow (introgression, hybridization) (Waldvogel et al., 2020) to explain and predict inbreeding, mutational load, diversity loss and responses to disease and management (*e.g.*, genetic rescue), ultimately guiding conservation actions (Hohenlohe et al., 2021; Schmidt et al., 2024; Theissinger et al., 2023). Over the last decades, major developments in theoretical (starting with (Hudson, 1983; McVean & Cardin, 2005a; Wiuf & Hein, 1999a, 1999b)) and simulation (Adrion et al., 2020; Baumdicker et al., 2022; Haller & Messer, 2019) approaches for population genomics, have allowed the development of methods to use full genome polymorphism data for the inference of past demographic and introgression events (Korfmann et al., 2023; Li & Durbin, 2011; Schiffels & Durbin, 2014; Sheehan et al., 2013; Terhorst et al., 2017; Wang et al., 2020). As a consequence, the fields of biogeography and population genetics are merging, allowing us to correlate past changes in the species/population demography and ecological niche (reconstructed via niche modeling methods) with past climatic data (obtained from geological records). Thereby, unprecedented insights are gained into the role of environmental and climatic

conditions in driving the evolutionary history of species, namely the demographic and selective events underpinning (local) adaptation to novel and changing habitats (Hohenlohe et al., 2021; Theissinger et al., 2023). Nonetheless, several pitfalls remain. First, the comparisons between the timing of these events estimated from genetic data and climatic ones remain inaccurate in species where life spans, mutation rates, or life-history traits are not known (Árnason et al., 2023; Freund et al., 2023; Lennon et al., 2021; Möst et al., 2015; Sellinger et al., 2020; Tellier et al., 2011). Second, the genetic architecture of selection (e.g. local adaptation) may range from selective sweeps at one locus (starting from one mutation) up to complex polygenic selection over many loci (with or without standing variation) (reviewed in Barghi et al., 2020). It is notoriously more difficult to detect footprints of selection in polymorphism data under polygenic selection rather than at single major loci (Barghi et al., 2020; Pavlidis et al., 2012; Sella & Barton, 2019). Third, past changes in population size, especially bottlenecks, can decrease the accuracy of genome scans for selection. Accurate demographic inference is thus required to subsequently improve the downstream inference of regions under selection in the genome (see the analyses in Soni et al., 2023 and recommendations in Johri et al., 2022). .

1.2 Population genomics theory and inference

However, the majority of statistical inference methods, based on neutral evolutionary models, are developed primarily for the inference of past demography and gene flow of human populations. Specifically, inference methods do assume human life-history traits such as diploidy, outcrossing, non-overlapping generations, and a small variance in offspring production. We argue here that these strong modeling assumptions are violated by many plant, fungal and invertebrate species. In spite of this, a handful of recent statistical inference methods allow us to move beyond these limitations and to broaden the applicability of population genomics methods. Realistic genomic features are also accounted for, such as variation in mutation and recombination rates along the genome (Barroso et al., 2019), and additional genomic markers (beyond Single Nucleotide Polymorphisms, SNPs) such as DNA methylation (Korfmann et al., 2024b; Sellinger et al., 2024). New methods also account for ecological and evolutionary (often overlooked) life-history traits such as seed banking and dormancy (Lennon et al., 2021; Tellier, 2019), self-fertilization

(Blischak et al., 2023; Daigle & Johri, 2025; Gilbert et al., 2022; Sellinger et al., 2020; Strütt et al., 2023), or large variance in offspring production (Árnason et al., 2023; Eldon, 2020; Korfmann et al., 2024a; Tellier & Lemaire, 2014). As a result of these advances, it is becoming possible to jointly estimate ecological parameters and past demographic events (Blischak et al., 2023; Gilbert et al., 2022; Sellinger et al., 2020; Strütt et al., 2023) as well as speciation (with or without gene flow) events (Dittberner et al., 2022). Applying appropriate methods accounting for life-history traits improves the inference accuracy of the past demographic history for a wide range of species (Árnason et al., 2023; Blischak et al., 2023; Korfmann et al., 2024a; Sellinger et al., 2020, 2021; Strütt et al., 2023). It is not the aim of this study to provide an in-depth review of statistical inference methods in population genomics and we thus redirect interested readers to (Dutheil, 2020; Ignatieva et al., 2025; Johri et al., 2022; Mather et al., 2020; Peede et al., 2025). In the following, we only sketch the general theoretical ingredients underpinning the inference of non-standard life-history and ecological traits, before suggesting new questions that can be addressed by extending such methodologies.

Simply put, the frequency and number of SNPs along the genome and their correlations can be summarized through the ratio of ρ over θ shaping the coalescent process (Hudson, 1983) and more specifically the so-called Ancestral Recombination Graph (ARG) (Griffiths & Marjoram, 1997). The population recombination rate $\rho = 4N_e r$ expresses the total amount of crossing-over (recombination) events in the diploid population of effective size N_e and depends on the per-site recombination rate r. The population mutation rate $\theta = 4N_e\mu$ is based on the effective size N_e (determining genetic drift) and the mutation rate μ. This ratio is important, as in the neutral theory of evolution, it defines the number of SNPs, their frequency, and the distance between recombination events along the genome (Linkage Disequilibrium, LD; or Identity By Descent, IBD, tracks; Hudson, 1983; Wiuf and Hein, 1999a). The genealogy, or coalescent tree, of a sample/population at a given locus is summarized by its length (time of coalescent events) and topology (order of branching; Griffiths and Marjoram, 1997; Tavaré et al., 1997). The time to the Most Recent Common Ancestor (TMRCA) of a coalescent tree depends on the population size (N_e), and can be estimated by the number of SNPs observed in the sample. Furthermore, recombination at the locus generates the ARG, which covers the full population history

of a chromosome, including all recombination and coalescence events. The ARG can be decomposed, for simplicity, as a series of coalescent trees linked by recombination events, or in other words, changes in tree topology along a sequence following a Markov process. This yields the Sequentially Markovian Coalescent (SMC) approximation (Li & Durbin, 2011; Marjoram & Wall, 2006; McVean & Cardin, 2005b; Wiuf & Hein, 1999a, 1999b). A portion of the genome (*i.e.* a locus) with a given ancestral genealogy (the coalescent tree) is thus delineated by two recombination events. The genealogical properties of a locus and transitions between loci are defined by the ratio ρ/θ, which are used in inference methods based on the ARG to estimate past demographic events (Li & Durbin, 2011; Marjoram & Wall, 2006; McVean & Cardin, 2005a). SMC-based inference methods are sensitive to the ratio ρ/θ departing from one, the value observed in humans, especially when $\rho/\theta > 1$. In the latter, there is an excess of recombination events which cannot be recovered because of the lack of information (Ishigohoka & Liedvogel, 2025; Sellinger et al., 2020, 2021). High ρ/θ ratios lead to inference inaccuracies due to two assumptions: 1) SMC-based methods are developed for humans and assume a value of this ratio close to 1, and 2) the methods further assume the value to be constant across the genome and through time, which may not be true in most species (Ishigohoka & Liedvogel, 2025; Sellinger et al., 2024). An important argument we develop in the following is that life-history traits influence this ratio (see Table 1 for an overview), and this influence can be understood and accounted for using recent inference methods.

1.3 Evolution of ecological traits in the age of population genomics

Most population models assume fixed and constant mutation and recombination rates as well as ecological life-history trait values in time, thus a constant ratio ρ/θ. Namely, a given plant species is expected to exhibit a fixed rate of dormancy or selfing since its evolutionary origin. This is, in part, a bias due to the study of evolutionary transitions at the macro-evolutionary level, thereby tracing the evolution of traits across phylogenies spanning millions of years (*e.g.* Willis et al., 2014 for dormancy, Duncan et al., 2024 for selfing). However, by definition, the evolution of an ecologically relevant life-history trait occurs over much shorter timescales of hundreds to thousands of years. The evolution of

Table 1: Overview of different life-history traits influencing population recombination (ρ) and mutation (θ) rates, when known. Baseline: random mating, no dormancy, obligate sex, discrete generations ($\rho_0 = 4Nr$, $\theta_0 = 4N\mu$). Entries show rescaling relative to baseline. For clonality, long life span and sweepstake reproduction, theoretical work is at times available for scaling the coalescent rate or recombination rate, but no intuitive formula could be provided (NA).

Life-history trait	parameter of the trait	ρ	θ	ratio ρ/θ
Selfing (Abu Awad & Billiard, 2017; Abu Awad & Roze, 2020; Brazier et al., 2025; Nordborg, 2000; Roze, 2009)	σ selfing rate[a]	$\frac{1-F}{1+F}$	$\frac{1}{1+F}$	$(1-F)$
Dormancy (weak seed bank)(Kaj et al., 2001; Lennon et al., 2021; Sellinger et al., 2020)	b germination rate	$\frac{1}{b}$	$\frac{1}{b^2}$	b
Clonality (Abdalrahem et al., 2025; Balloux et al., 2003; de Meeûs & Balloux, 2004; Halkett et al., 2005; Hartfield et al., 2016)	clonality rate	NA	NA	NA
Long life-span (Alexandre et al., 2025; Charlesworth, 1994)[b]	d death rate at each time step	$\frac{(N-1)}{d(2N-1-dN)}$	$\frac{1}{2-d}$	$\frac{(2-d)(N-1)}{d(2N-1-dN)}$
Sweepstake reproduction (Birkner et al., 2013; Eldon, 2020; Schweinsberg, 2003)	α parameter of β-coalescent[c]	NA	$\left(\frac{\alpha\beta(2-\alpha,\alpha)}{m^\alpha}\right)^{1/(\alpha-1)}$	NA

[a] $F = \sigma/(2-\sigma)$ (inbreeding coef.). Note that the scaling by F breaks down with high selfing and recombination rates (Roze, 2009). [b] A. Tellier unpublished data. [c] $1 + \frac{1}{(\alpha-1)2^{\alpha-1}}$

life-history traits occurs as a cause or consequence of changes in climatic conditions, abiotic factors and landscape characteristics which define 1) biotic and trophic interactions, 2) spatial structure, 3) positive selection pressure for local adaptation, and 4) fluctuating selection pressures (see Figure 1). In order to apprehend the impact of the future climatic, landscape and habitat changes on species resilience and adaptation, we argue for a more precise investigation of how life-history traits change over population genetics timescales of tens to thousands of generations.

In the plant literature, there is a wealth of theoretical and empirical studies dissecting the causes and consequences of transition from outcrossing to selfing (see the recent Abu Awad and Billiard (2017), Abu Awad and Roze (2020), and Brazier et al. (2025) and references therein). For example, selfing promotes the survival of populations at the margin of species ranges, and thus favours the establishment of populations during the colonization of novel isolated habitats (Pannell, 2016). The presence of a constant selfing rate within one or between several populations can be inferred along with the demographic history and distribution of fitness effects of mutations (Blischak et al., 2023; Dittberner et al., 2022; Gilbert et al., 2022; Sellinger et al., 2020 but see Daigle and Johri, 2025 for possible biases). However, to our knowledge, so far only one pioneering method allows the inference of changing selfing/outcrossing rate in time (Strütt et al., 2023). The main finding of that study is that the transition from outcrossing to selfing is observed by studying the transitions in TMRCA of consecutive coalescent trees (and the genomic span of a tree) along the genome (Figure 2). 1) Transitions can occur in recent times between short coalescent trees that exhibit low nucleotide diversity and span relatively long genomic regions (hundreds to thousands of bp) due to the low effective recombination rate under the selfing regime. 2) Transitions between old coalescent trees that exhibit high nucleotide diversity and span very short genomic regions (tens of bp) because of the higher recombination rate under the outcrossing regime. This information is reflected as substructuring in the density of the so-called transition matrix, which summarizes changes in coalescent times along the genome (see below). In other words, polymorphism data exhibit unusual clustering patterns of mutation (SNPs) and recombination events along the genome upon a change of the ratio ρ/θ in time (Strütt et al., 2023). We note also that such structuring in the transition matrix can also occur due to changes in the ancestral

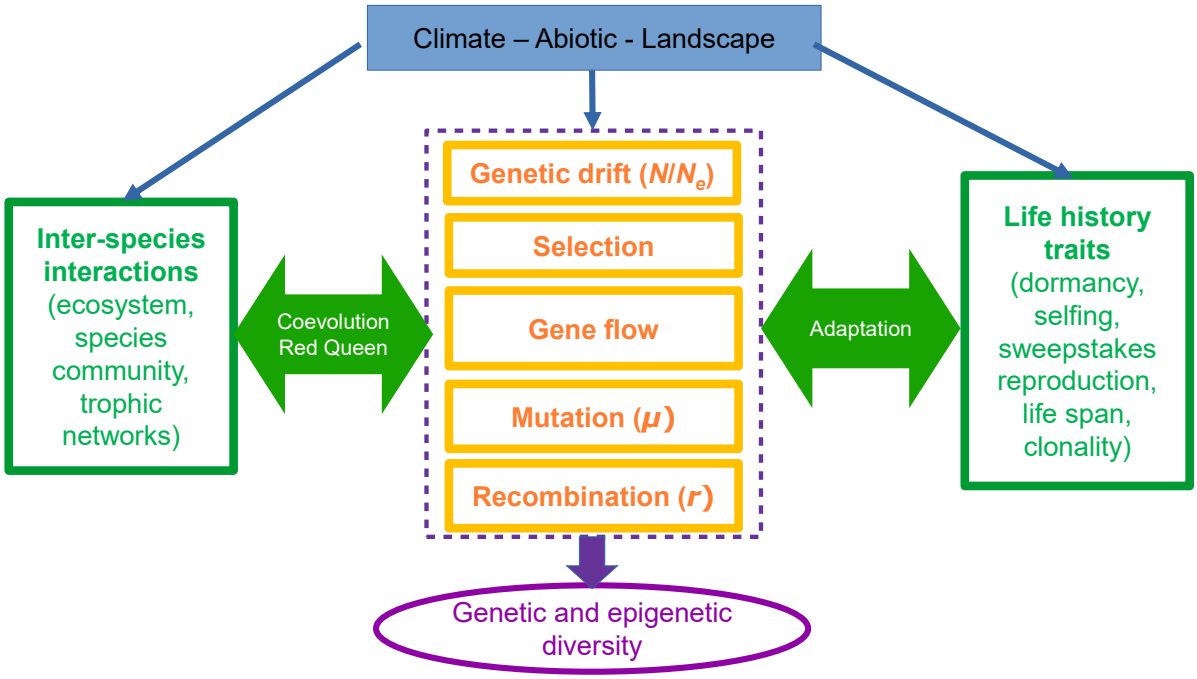

Figure 1: Schematic of interactions between ecological and evolutionary forces upon changes in the abiotic environment and landscape (top box). Environmental modifications trigger neutral and selective changes in the evolvable parameters of the species interactions (green box on the left) and in the ecological life-history traits (green box on the right), via conventional evolutionary forces (orange). The evolutionary forces under the influence of ecological life-history traits generate observable polymorphism patterns in the genome and define the genetic and epigenetic diversity (purple).

population spatial structure (Cousins et al., 2025; Nieto et al., 2025; see below for a discussion of non-identifiability).

It is a central hypothesis and argument of this manuscript that inference of the ratio ρ/θ in time by means of population genomics can, therefore, help reveal the timing of changes in life-history traits and population structure (Cousins et al., 2025), and highlight possible links of causality with environmental changes. We further suggest leveraging genome-wide polymorphism data from plant populations to study additional eco-evo feedback processes, such as niche construction and species interaction networks. In the following, we first highlight how ecological and environmental changes can drive the evolution of important and common plant life-history traits and how such adaptations affect the ratio ρ/θ (Figure 1, Table 1). Second, we describe extensions of inference methods that could be used to reconstruct this evolutionary history.

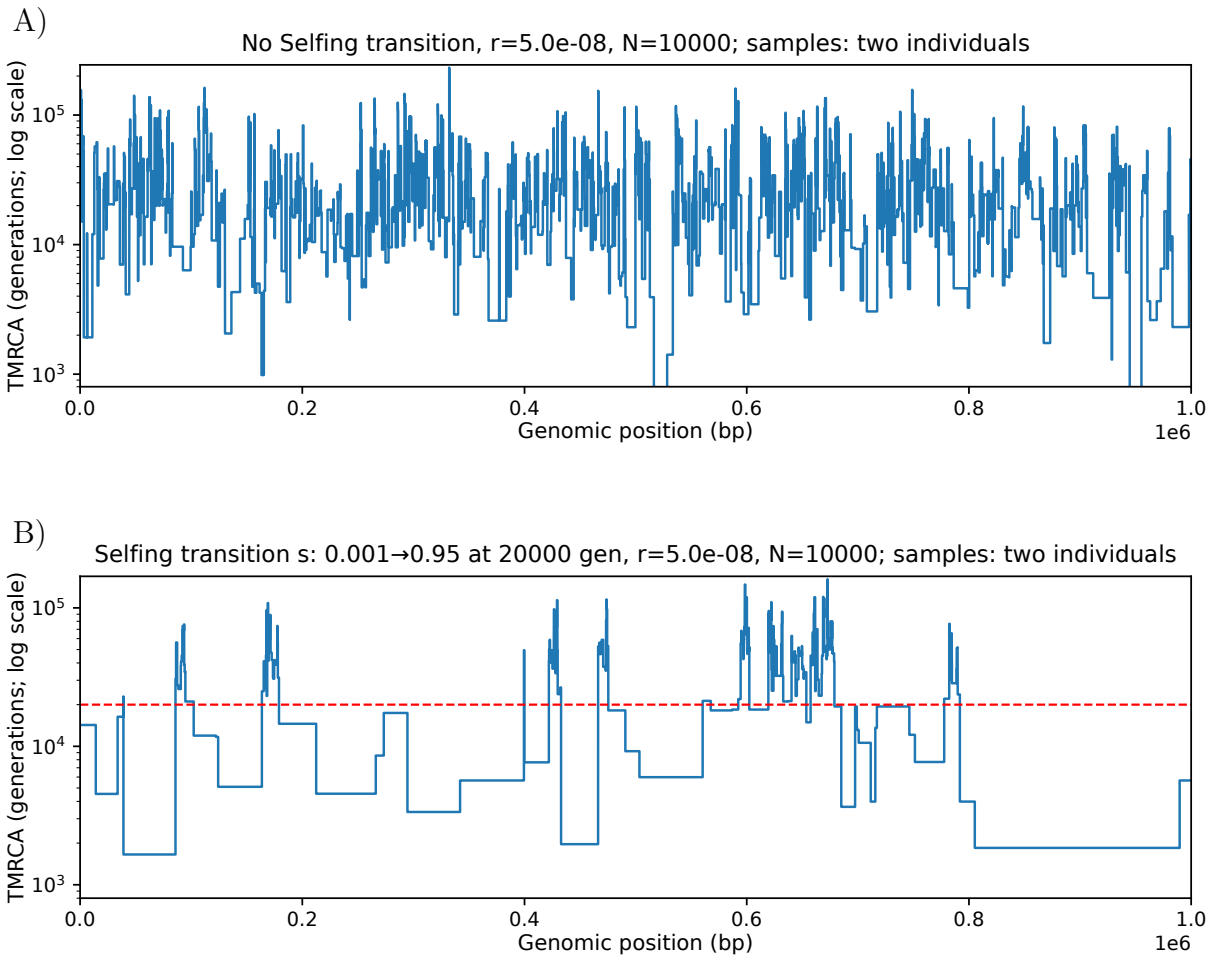

Figure 2: Comparison of genome-wide TMRCA patterns for two haploid samples from distinct individuals. A) Constant outcrossing (no transition; constant s=0.001). B) Transition from outcrossing to high selfing during the final 20,000 generations before sampling (s : 0.001 $\rightarrow$ 0.95). The blue step curve shows the TMRCA of the two lineages along the genome; steps occur at recombination breakpoints. The dashed red line marks the transition time. (Y-axis is on log scale.) *Brief methods:* We simulated diploid populations forward in SLiM (Haller & Messer, 2019) with time-varying selfing rate and tree-sequence recording on. The recorded genealogies were recapitated with msprime (Baumdicker et al., 2022) (ancestral $N_e = 10{,}000$, recombination rate $r = 5 \times 10^{-8}\,\mathrm{bp}^{-1}\,\mathrm{gen}^{-1}$), and neutral mutations were added at $\mu = 10^{-8}\,\mathrm{bp}^{-1}\,\mathrm{gen}^{-1}$. For each panel we computed TMRCA along the genome between two haploid genomes (one from each diploid individual) using tskit (Kelleher et al., 2016).

2 *The known unknowns*: Causes and consequences of changes in eco-evo traits

2.1 Change in life history traits which decrease the ratio N_e/N

Several life-history traits such as clonality, selfing, longer life-span (and generation overlap) and sweepstakes reproduction decrease the ratio N_e/N (Waples, 2025; Waples et al., 2013). In other words, the census (or ecological abundance) size of the population (N) appears much higher than its effective population size (N_e), the latter reflecting the amount of genetic drift and nucleotide diversity (Charlesworth & Charlesworth, 2010).

Generation overlap promoted by long life spans decreases the N_e versus the population size N because few individuals effectively reproduce each generation compared to the total size N (Alexandre et al., 2025; Charlesworth, 1994; Waples, 2025), and consequently decreases the population recombination and mutation rates. Nonetheless, the lower expected population mutation rate can be compensated by an inflated mutation rate per individual, if the mutational output increases during the life span of the plant (for example, possible mutations between branches of a tree plant; Antolin and Strobeck, 1985; Iwasa et al., 2024).

Similarly, as a first approximation, clonality in plants, invertebrates or fungi results in a low effective population size as few lineages are found in the present time (see Table 1, Hartfield et al. (2016)). However, we note that the effects of clonality on mutation, drift and recombination can generate more complex scenarios and outcomes in terms of underpinning coalescent trees, especially for very high rates yielding high within-individual diversity (Abdalrahem et al., 2025; Halkett et al., 2005; Hartfield, 2021; Hartfield et al., 2016). Clonality may evolve as a reproductive assurance strategy in crop pathogens (as in the pathogen of potato and tomato, *Phytophthora infestans* (Ludwiczewska et al., 2025)) or plants with long-lived survival strategies (for example, as ramets connected by stolons or rhizomes (Franklin et al., 2021; Klimešová et al., 2021)).

Meanwhile the effect of selfing is to decrease N_e by at least a factor two (accounting for background selection can result in much lower N_e; Roze, 2016) and diminish the effective recombination rate (Table 1, Nordborg (2000)) but in contrast to clonality, high selfing rates decrease heterozygosity.

Finally, sweepstakes reproduction occurs in species producing a large number of offspring

per parent (of the order of the population size) but exhibiting a (very) low survival rate of juveniles to the next generation. This high amount of seeds, spores, or propagules promotes reproductive assurance (so-called ecological K strategy or type III survivorship) and is possibly common to airborne plant pathogens or plant species with short life cycles (Freund et al., 2023). A relationship between the propagule number and size, and genetic diversity has been shown in invertebrate animal species (Romiguier et al., 2014; Waples et al., 2013). Sweepstakes reproduction also decreases the ratio N_e/N (Árnason et al., 2023; Eldon et al., 2016; Freund et al., 2023; Tellier & Lemaire, 2014; Waples, 2025).

We now propose a set of general predictions on the timing, speed, and likelihood of the evolution of these life-history traits, which can be tested. On the one hand, clonality and selfing can frequently appear in fungi (*e.g.* fungal pathogens of plants) by mutations or loss of the mating-type genes as observed in crop pathogens, which can exhibit some clonal lineages with one type (Ludwiczewska et al., 2025). Fungi, especially pathogens of plants, do present the ability to produce large amounts of dispersing and infectious spores, making them likely to exhibit sweepstakes reproduction (Tellier & Lemaire, 2014). This is especially true for crop pathogens, in particular, which exhibit frequent boom and bust cycles, selection due to fungicide treatment, seasonal bottlenecks and a great influence of the climate on their infection rate (Jigisha et al., 2025; Tellier & Lemaire, 2014). The evolution of selfing in plants is relatively common by mutation of the self-incompatibility genes (Charlesworth et al., 2005; Pannell, 2016). Thus, clonality/selfing/sweepstakes reproduction may emerge relatively rapidly through genetic modifications and be subsequently selected by environmental changes, leading to sharp temporal transitions in reproduction mode. For example, we speculate that clonal pathogens currently infecting crops may have originally infected wild species with fewer annual clonal cycles (or outcrossing) due to unfavorable conditions and limited resource availability. Transitioning to crop hosts, with their abundant and more favorable conditions (a longer growing season), could have increased their clonal reproductive cycles. Such a transition in clonality rates could coincide with the advent of agriculture and the domestication of crops and livestock. The speed of evolution of such traits may be similar to transitions in outcrossing/selfing rates, which, in families of flowering plants with self-incompatibility, occur through a mutation at a self-incompatibility locus. Transitions to selfing are punctual events (Strütt et al.,

2023) which are uncovered when studying recent population/splits (less than a million years ago, for example in *Arabis sp.*; Dittberner et al., 2022 and *Capsella sp.*; Koenig et al., 2019), or population dynamics at the species margins (Pannell, 2016). Thus, we speculate that studying the population genomics of recent population split or population expansion in new habitats (including agricultural landscape) would reveal more cases of transition in life-history traits (and their genetic bases) beyond the known cases of outcrossing/selfing in plants.

On the other hand, we note that the evolution of the same traits, long life-span, clonality and sweepstakes reproduction in plants also requires specific physiological mechanisms of reproduction and vegetative multiplication: for example, the existence of ramets and rhizomes, perennial physiological structures or the production of large amounts of pollen in gymnosperms. We speculate that in these cases, the changes in life-history trait may be more gradual and occur over longer periods of time beyond a few hundreds/thousands of generations via the evolution of novel physiological pathways and rewiring of gene networks. Such life-history traits change may be better revealed using functional phylogenomic comparisons between species (see Delaux et al., 2019 for an overview).

2.2 Dormancy and dispersal as bet-hedging strategies which increase the ratio N_e/N

Dormancy and dispersal (of pollen or seeds) are well-known plant bet-hedging strategies in space and time, respectively (Buoro & Carlson, 2014; Vitalis et al., 2013). In particular, dormancy (long-term seed banking) evolves in response to unpredictable habitats (*e.g.* desertic, (Adondakis & Venable, 2004)), competition (Blath & Tóbiás, 2020) or to coevolution with antagonistic species (Verin & Tellier, 2018), and has important consequences for the genetic diversity and evolutionary potential of populations (Lennon et al., 2021; Tellier, 2019). Dormancy delays the time to fixation or loss of alleles as alleles in the seed bank are hidden from genetic drift (the diversity storage effect of dormancy, Kaj et al., 2001; Lennon et al., 2021; Tellier, 2019). As a result, dormancy lengthens the TMRCA of a population, allowing for the inference of older demographic events than would be possible in the absence of seed banking (Möst et al., 2015; Sellinger et al., 2020; Živković & Tellier, 2012). Concomitantly, seed banking increases the effective population size N_e

relative to the census size N, as encapsulated for the weak seed bank by the formula $N_e = N/b^2$, with $0 < b < 1$ being the germination rate (Kaj et al., 2001; Tellier et al., 2011). Simultaneously, the recombination rate is multiplied by the germination rate (b) because only active above-ground plants can perform meiosis (so that $\rho = 4N_e rb$). Overall, seed banking with smaller values of germination rate (b) decreases the ratio $\rho/\theta = rb/\mu$ for fixed r and μ values (Sellinger et al., 2020; Živković & Tellier, 2018). Long-term dormancy is widespread across plant species, though it is unclear at what speed it evolves. Most seeds of land plants have the ability to stay dormant, but long-term dormancy also entails the ability to remain dormant even if conditions are favourable (Baskin & Baskin, 2000). Different physiological and morphological adaptations are necessary for long-term dormancy. The so-called morphophysiological dormancy is likely ancestral to all seed plants (Willis et al., 2014). The appearance of several types of dormancy likely evolved from this ancestral state, such as morphological, physiological, physical dormancy and nondormancy (Willis et al., 2014). However, it remains unknown how rapidly such transitions in dormancy rates occur, and whether variations in dormancy rates across populations of a given species are neutral, adaptive or maladaptive (Lampei et al., 2017; Tomiolo et al., 2015). We thus advocate that novel inference methods can be used to test for recent timing of dormancy adaptation in plants.

Similarly, gene flow between populations of a metapopulation, namely the dispersal ability, is a (neutral, adaptive or maladaptive) trait that evolves and varies across land plants (Vitalis et al., 2013) and which can be negatively correlated with dormancy (Buoro & Carlson, 2014). The rate of gene flow and the contribution of each sub-population to offspring production determine the effective population size of a metapopulation (N_e) based on the local population sizes (N) of each sub-population (deme). If all demes contribute similarly to the offspring production, low levels of gene flow increase N_e compared to the sum of all local N values because genetic differentiation increases between demes (Caballero, 2020; Charlesworth & Charlesworth, 2010). Changes in dispersal rates, or in offspring production between demes, are in part adaptive and a response to environmental pressures such as habitat fragmentation, changes in species range and niche due to abiotic and biotic factors. Changes in time of gene flow between demes or in the population spatial structure (deme sizes, number of demes, existence of gene flow between demes) is

reflected in changes in the ratio N_e/N over time, the ratio ρ/θ and the sub-structuring of the transition matrix (Cousins et al., 2025). The principle for inference of changes in gene flow and/or spatial structure in time is based on inferring the ratio between the cross-population and within-population coalescence rates per hidden state (time interval) (Schiffels & Durbin, 2014). This relative cross coalescence rate measures genetic exchanges between historical populations, and is expected to be close to one when the two populations are effectively one panmictic unit (for example under high gene flow), and close to zero when populations are fully separated (under very low gene flow). It is important to note that changes in gene flow and/or spatial structure can be confounded with one another and with changes in N_e in time (Chikhi et al., 2018; Mazet & Noûs, 2023). There is thus some amount of non-identifiability between models of changes in rates of gene flow, changes in ancestral spatial structure, and population size variation (N_e)(Chikhi et al., 2018; Cousins et al., 2025; Jouniaux et al., 2026; Mazet & Noûs, 2023), leading to different interpretations regarding the reason for the observed shared polymorphism between species (Tournebize & Chikhi, 2025): namely, introgression or shared ancestral polymorphism (due to population structure, see below for further discussion on non-identifiability).

2.3 Changes in mutation and recombination rates

A major assumption of all statistical inference methods is that the per-site mutation (μ) and recombination (r) rates are constant in time and follow a homogeneous Poisson process along the genome(Johri et al., 2022; Sellinger et al., 2024; Soni et al., 2023, 2024). Accounting for variation in these rates along the genome can be done by using empirical rates (mutation or recombination maps if available), or for example, by a first round of inference via iSMC (Barroso et al., 2019) and a second round of demographic inference for windows of given estimated rates. If the assumptions of Markovian and Poissonian properties along the genome and in time are not met, the accuracy of the inference decreases as the fundamental hypotheses of the coalescent model are violated (Soni et al., 2023, 2024). This phenomenon was discussed and highlighted when using gene body methylation data in *Arabidopsis thaliana* for demographic inference, or for assessing the reliability of selective sweep scans (Johri et al., 2022; Soni et al., 2023) or estimation of the distribution of fitness effects (Soni et al., 2024). Regarding methylation, the property of cytosine

methylation to mutate per site but also over genomic regions (group of cytosines) violates the model assumption and yields problematic results in the SMC (Sellinger et al., 2024). An imperfect but practical solution is to use only polymorphic methylated sites (Single Methylated Polymorphisms) within coding genes (Vidalis et al., 2016) to perform demographic inference using SMC (Sellinger et al., 2024) or Deep Learning methods (Korfmann et al., 2024b). To make use of full genome data, additional markers such as microsatellites, methylation, indels (insertion-deletions), if they fulfill the mentioned assumptions, can be used to increase the statistical power to infer past demographic events as well as changes in ρ/θ (Sellinger et al., 2024).

Furthermore, we note that the per-site mutation and recombination rates are also subject to evolutionary change. In fact, these rates are under constraint and depend on the strength of selection to maintain them at reasonable levels. This is termed the drift barrier hypothesis (Sung et al., 2012), which is one hypothesis for the evolution of the mutation rate. The rates are evolving based on the balance between the advantages and disadvantages of higher mutation and recombination rates (Barton, 2010; Sung et al., 2012). We speculate here that changing life-history traits and the ratio N_e/N affects the efficacy of selection in controlling the mutation and recombination rates. Changing life-history traits such as clonality, selfing, life-span, sweepstakes reproduction or dormancy would in turn affect the genomic control for optimum per-site mutation or recombination rates (thus the reciprocal arrows in Fig. 1): this has been theoretically explored in the case of selfing (Gervais & Roze, 2017; Stetsenko & Roze, 2022). Such subtle changes due to eco-evo feedback loops may be detected by estimating the empirical per-site rates r and μ at present, and comparing these to the inferred ratios ρ/θ over time. The statistical accuracy of such analyses is yet unknown.

2.4 *Unknown unknowns*: from the extended phenotype to community eco-evo genomics

We have focused on changes in ecological life-history traits decreasing or increasing the ratio N_e/N. Such changes not only influence patterns in genome transmission but are the results (or the consequences) of species adaptation to the environment (Figure 1).

Furthermore, changes in life-history traits can, in return, modify the abiotic and biotic environment itself. Evolutionary mechanisms such as the extended phenotype (Dawkins, 2016) or niche construction (Odling-Smee et al., 2013; Scott-Phillips et al., 2014), rely on adaptation by organisms to modify not only their biotic but also their abiotic environment: for example, changes in soil texture and soil microbiome due to earthworm activity and plant roots. These changes are not without consequences, either from the point of view of a focal plant species or from the point of view of several interacting species, and thus changes percolate to higher levels of biological organization (species community up to ecosystems). We envision three examples of environmental changes and eco-evolutionary feedback in multi-species systems. First, plant transition from outcrossing to selfing can promote the colonization of new habitats (Pannell, 2016), accompanied by a founding event and a possible novel population spatial structuring. In doing so, the abiotic and biotic habitats are transformed by the presence of the selfing plant species, potentially facilitating the colonization by other plant and invertebrate species, paving the way for new species community compositions and the evolution of new trophic levels. This scenario assumes, therefore, founder events and possible changes in life-history traits for each species, which we suggest can be detected by applying inference methods on full genome polymorphism data (see below). Second, at the scale of species communities, changes in the abiotic environment (say, an extended drought period or a glacial age) could promote simultaneous and/or correlated responses in adaptive traits across different plant species. For example, a study reveals the joint demographic response of plant and insect species of the Eurasian steppe biota to environmental changes (Kirschner et al., 2022). This exemplifies that plant species in a community do show correlated demographic responses to habitat change. Third, eco-evo dynamics occur in a multi-species community. A specific case is co-evolution between antagonistic species (hosts and parasites, prey-predators), which is expected to yield co-demographic changes in both species at short and long-term time scales (Živković et al., 2019). A first attempt to capture such multi-species co-demographic history has been made using inference from SMC methods and correlating N_e of the host and pathogen populations at different time steps (Hecht et al., 2018, 2020). We suggest below extensions of the existing inference methods to infer co-demographic, co-evolutionary and co-structure changes for multi-species communities, thereby dissecting the causes and consequences of eco-evo feedback over time.

3 Inference methods to reveal the *unknowns*

We highlight some inference methods to estimate demographic events and possible changes in ecological life-history traits in single or assemblage of species, as well as future developments needed. From a conceptual point of view, we assume that time in the past is split into discrete periods, each of which is characterized by a given value of the life-history trait per species, namely a given ratio ρ/θ, which is to be estimated.

3.1 SMC based methods

Methods based on the Sequentially Markovian Coalescent (SMC) (McVean & Cardin, 2005b) make use of Hidden Markov Models (HMM), where the observed genetic data (SNPs) are considered to be a signal produced by an underlying unobservable genealogy. The genealogy is modeled as a series of hidden states in a Markov process. A key component of this process is the estimation of the so-called transition matrix, which contains the predicted transition probabilities from one hidden state to another. It reflects the likelihood of transitioning from one coalescent tree (with a given TMRCA) to the next tree (along the genome) by recombination. Each coalescent tree depends only on the tree at the previous position along the genome, leading to a computationally simplified process. We refer to several reviews on SMC methods for more details on the computations (e.g. Dutheil et al., 2009; Ignatieva et al., 2025; Mather et al., 2020; Peede et al., 2025; Spence et al., 2018) and recommendations for analyses (Hilgers et al., 2025; Sellinger et al., 2021). The transition matrix is thus a summary of the changes of genealogies and coalescent trees along the genome. The structure of the transition matrices, that is the density of observations, is determined by past changes in demography as well as ecological life-history traits affecting the ratio ρ/θ as shown for transition to selfing (Strütt et al., 2023) and changes in population structure (Cousins et al., 2025; Nieto et al., 2025). SMC-based methods are thus methods of choice to infer changes in ecological life-history traits in time per species.

A first inference of co-demographic or co-evolutionary history between species can be

performed by correlating the population sizes N_e at different time points (hidden states) for different species based on independent specific inferences (Hecht et al., 2018, 2020). The accuracy of such comparisons relies on the correct scaling of the generation time and mutation rate to match between the studied species. We suggest to go one step further by directly correlating the densities of coalescent times (TMRCA) in the transition matrix for each studied species. Using a likelihood approach (or other algorithms), one should be able to obtain an estimate of the correlation between demographic histories across multiple species for which full-genome polymorphism data are available. In the case of closely related sister species, this multi-species SMC outcome could be compared to the results from multi-species coalescent analyses. We speculate that a similar analysis could be performed using also the density of cross-coalescent rates at different hidden states between populations of each species in order to detect changes in the species' spatial structure. The advantage of using the transition matrix (and density of IICR) is that time is already scaled by the underlying coalescent framework, allowing comparisons across species independently of knowing the generation and mutation rate. Extensions of SMC methods to analyze multi-species data would therefore allow for a preliminary inference of the important co-demographic and co-evolutionary (life-history traits) changes in several species of the community, albeit not demonstrating the underlying causal eco-evo mechanism.

3.2 Approximate Bayesian Computation methods

In principle, the information contained in the transition matrix (IICR and cross-coalescent rates) can also be used in other inference methods such as Approximate Bayesian Computation (ABC) (Strütt et al., 2023) or deep learning (Korfmann et al., 2024b), especially when the analytical computation of the transition and emission probabilities for the HMM is difficult to obtain. The term "approximate" highlights that the method does not rely on a direct likelihood function (Beaumont et al., 2002; Tavaré et al., 1997). In ABC methods, the explicit computation of the likelihood $P(D|\theta)$ is replaced with an approximate approach. This is because, for models with complex and multiple demographic events, the likelihood is often difficult or even impossible to compute directly. Instead, ABC methods rely on generating simulated data similar to the observed data and measuring the distance between the simulated and real datasets. Polymorphism data are thus summarized

using a set of summary statistics computed on simulated and real data. The model fit is then obtained by matching large sets of simulated statistics with those derived from real data (Beaumont et al., 2002; Csillery et al., 2012). The choice of summary statistics being crucial for ABC performance, well-tested and useful sets of summary statistics and strategies for selecting these exist (Csillery et al., 2012; Jay et al., 2019), with the latest utilizing random forest (RF) methods (Pudlo et al., 2016; Raynal et al., 2019).

Table 2: Overview of genome-wide and per gene statistics that can be used for ABC inference of co-demographic or co-evolutionary history in a multi-species system, assuming samples from different species containing numerous genomic windows of fixed size spread across the genomes (e.g. Jay et al. (2019), Märkle and Tellier (2020), Pudlo et al. (2016), and Raynal et al. (2019)).

Statistic	Signal	Role for eco–evo inference	Typical summary
Classic population genetic			
Segregating sites (S)	Mutation rate	Baseline level of diversity; used for $N_e(t)$	Mean and variance of S across windows
Watterson's $\hat{\theta}_W$	Scaled polymorphism	Helps disentangle demographic (N_e) changes	Mean, variance across windows
Pairwise diversity $\hat{\theta}_\pi$	Average coalescent time	Helps disentangle demographic (N_e) changes	Mean, variance across windows
Tajima's D	Site-frequency spectrum skew	Detects recent growth or bottlenecks; selection vs demography	Mean, variance across windows
LD decay (r^2 vs distance)	Recombination and demography	Helps in detecting ρ and hence life-history traits affecting effective recombination	Mean r^2 in distance bins; slope of decay
Joint SFS (multi-population)	Population splits and migration/introgression	Detects time-varying dispersal and range shifts	Binned counts for each frequency class
Pairwise F_{ST} and D_{XY}	Differentiation and divergence	Relates spatial structure to N_e/N and life-history changes	Genome-wide values and window distributions
ARG / SMC-derived			
Mean local T_{MRCA} (from ARG/SMC)	Coalescent history	Directly estimates time-varying N_e and hence dormancy/selfing effects	Mean, variance and quantiles across windows or trees
Transition matrix of TMRCA states	Heterogeneity in genealogies along the genome	Captures signatures of mating-system shifts, spatial structure, sweepstakes	Row-normalised counts of transitions between time bins
Two-site SFS	Deviations from Kingman coalescent	Distinguishes multiple-merger coalescents (sweepstakes) from standard models	Binned joint frequencies for pairs of SNPs (Fenton et al., 2025)

In addition to classic population genetic (genotypic) statistics, it is now possible to incorporate coalescent statistics into an ABC framework, thus summarizing more accurately the variation of genealogies along the genome. More precisely, for our purpose, coalescent statistics should summarize more accurately the ARG and thus the influence of ρ and θ on

the distribution of SNPs and their LD. It is thus important to choose a large region of the genome with sufficient coalescent trees to capture regions with different ρ/θ ratios (Strütt et al., 2023). In Table 2 we list a set of statistics that we consider particularly useful for eco–evo questions discussed here, together with their main signals. The main advantage of ABC is that it can allow for the simulation of precise eco-evo scenarios, meaning to gain insight into possible causal relationships between changes percolating across the community. For example, one can draw simultaneous inference of the parameter of coevolution between hosts and their parasites based on *ad hoc* mathematical models (Märkle & Tellier, 2020; Nuismer & Week, 2019; Nuismer et al., 2022; Tellier et al., 2014; Živković et al., 2019). We suggest developing ABC based on 1) genome-wide polymorphism statistics to decipher the co-demographic history of hosts and their parasites (Živković et al., 2019), and 2) gene-specific statistics to uncover genes underpinning host-parasite interactions (Märkle & Tellier, 2020; Märkle et al., 2024). While the mentioned ABC methods focus on pairs of interacting species, the ABC framework can, in principle, accommodate multi-species community-level mathematical and stochastic models and the resulting large set of statistics across species. The flexibility of the ABC framework and especially the model-choice step can be used to test for the occurrence of co-demographic history, co-changes in population structure, or co-evolution in life-history traits (e.g. sweepstake reproduction in parasites) for specific models of interactions (accounting for trophic network, parasitism, commensalism, and mutualism). Using the relevant co-demographic and co-evolutionary histories as a baseline for the genomic background, a second round of ABC analysis can then focus on deciphering the genes underpinning parasitic or mutualistic interactions across pairs (or perhaps triplets) or species.

3.3 Inference with deep learning

New developments in the field of deep learning have opened the way for novel inference using many samples and inference of the TMRCA of a sample along the genome (*e.g.* (Korfmann et al., 2024a, 2025; Speidel et al., 2019). Deep Learning methods for population genomics inference (reviewed in Korfmann et al., 2023) can also be trained on genotypic data (Convolutional Neural Networks, CNN, (Sanchez et al., 2021; Sheehan et al., 2013)), on an empirical transition matrix built using the statistics θ_W (Watterson's estimator) as a proxy for the TMRCA (Korfmann et al., 2024b), or directly on the

inferred coalescent trees (Korfmann et al., 2024a). A pioneering study used a combination of CNN and ABC based on restriction-site associated DNA sequencing (RADseq) revealed the common demographic response to environmental changes of two angiosperm and three insect Eurasian steppe species (Kirschner et al., 2022). To move beyond correlations and dissect the possible mechanisms underlying common changes in multi-species communities, we suggest expanding deep learning to test and infer co-demographic and co-evolutionary scenarios based directly on distributions (and transition matrices) of TMRCA along the genomes of the studied species. Furthermore, one could in a second step scan the genomes of the different species to reveal gene trees (topology and TMRCA) correlated with environmental responses, and thus pinpoint genes involved in these adaptations. The advantages of the deep learning method are that 1) they can be trained on sets of tested models (Adrion et al., 2020) which can be expanded to multi-species systems, and 2) these are flexible with regard to sample size and the stochastic noise in the polymorphism data (Korfmann et al., 2023, 2025).

3.4 Additional markers may increase the inference accuracy

With the advances in full genome sequencing, especially long read sequencing, it has become feasible to integrate several types of genetic (SNPs) and epigenetic (DNA methylation) markers for evolutionary inference (Korfmann et al., 2024b; Sellinger et al., 2024). In principle, other markers such as microsatellites and indels can also be added (Ignatieva et al., 2025). As these markers exhibit a wide range of mutation rates, the resolution of past inference would be improved across a larger time span than can be done based on SNPs alone (Sellinger et al., 2024). ABC and deep learning methods are well-suited to integrate additional markers to infer changes in ecological life-history traits based on an empirical transition matrix or inference of the coalescent trees. An additional advantage of ABC and Deep Learning is the possible integration of several types of samples, for example, temporal data obtained from ancient DNA or museum samples, which can be integrated in the coalescent simulations and training set. Integrating such heterogeneous datasets in time is challenging but would be expected to enhance the resolution of the transition matrix and of the inference of co-demographic and co-evolutionary history. Such data provide time sample series with known dating and are thus useful in tracking

genetic changes and allele frequencies in host and parasite populations (Živković et al., 2019). The analyses we highlight would open the fascinating insights into how ecological and evolutionary mechanisms feedback with the environment to drive adaptive changes across interacting species. The inference of changes in ecological life-history traits and their timing across several species of a given community, and across trophic levels, can then be linked to environmental changes to understand how species networks change in time.

3.5 Limitations of inference methods

Nonetheless, we wish to finish with a word of caution on the expected difficulty in conducting and interpreting such inferences. First, such inference can only point out the possible co-occurrence of events, even when using ABC or deep learning model test, but cannot prove the ultimate causation between events. Second, like any statistical inference method, they yield confidence intervals in their estimates (of N_e and of the timing of events; Bansal and Nichols, 2025; Hilgers et al., 2025), which should be carefully interpreted when compared to estimates from past climatic conditions (and past niche modeling predictions). Third, several changes in life-history traits as well as demographic events can yield similar effects (or compensate one another) on the genomic polymorphism data, so that non-identifiability of complex past events may remain a challenge despite the wealth of new data. In other words, polymorphism data exhibit unusual clustering patterns of mutation (SNPs) and recombination events along the genome upon a change of the ratio ρ/θ in time (Strütt et al., 2023). Such structuring in the transition matrix can also be due to changes in the ancestral population spatial structure (Cousins et al., 2025; Nieto et al., 2025), which can yield wrong interpretation of the introgression patterns between species (Chikhi et al., 2018; Tournebize & Chikhi, 2025). Additional work is thus needed to disentangle between confounding factors in the estimation of N_e in time. We suggest, for example, to combine statistics based on the transition matrix with other classic population genetics statistics (Table 2) using the ABC or deep learning framework, which may prove more powerful than the SMC and IICR methods for in-depth analysis of co-demographic and co-evolutionary scenarios. Finally, we caution about the influence of selection in the genome on the accuracy and outcome of inference. Indeed, background selection (due to linkage with sites under purifying selection) as well as hitch-hiking and

genetic draft (due to linkage with sites under positive selection) do affect the accuracy of past demographic inference (Daigle & Johri, 2025; Hilgers et al., 2025; Johri et al., 2022; Soni et al., 2023, 2024). We note that the effect of linked selection on inference accuracy does change depending on the considered life-history trait and its influence on the ratio ρ/θ. For example, on the one hand, dormancy is expected to decrease linkage effects around sites under selection (yielding weaker background selection and genetic draft)(Živković & Tellier, 2018). On the other hand, selfing enhances the effect of linked selection (Roze, 2016), thus likely decreasing the accuracy of past demographic inference (Daigle & Johri, 2025; Strütt et al., 2023). The results of inference of co-demographic and co-evolutionary histories need to be critically evaluated using regions with various recombination and mutation rates, especially in communities or assemblages containing species with different life-history traits, generation times, and genomic characteristics (genome size, gene density, proportion of transposable elements).

4 Conclusions

The developed research avenues are key to fully develop an explanatory and predictive science of conservation biology at the scale of individual species and species networks/communities in times of global changes (climatic, landscape, habitat). The first consequence is that we are now able to better understand changes in ecological and life-history traits in the past and their correlation with past climatic events; thus demonstrating the tight feedback loop between changes at the evolutionary and ecological levels, and their consequences on genome evolution. The second consequence is that we can also infer ecological and life-history traits predominantly affecting genome evolution of species and thus better predict species' adaptive potential in the face of climate change and habitat fragmentation. The third consequence is to extend our framework to community genomics perspectives (host-pathogens, host-mutualists, species communities and trophic networks). The type of approach we suggest to develop is still in its infancy, and further developments will require inter-disciplinary collaborations between plant ecologists, evolutionary biologists, population geneticists, mathematicians and statisticians to embrace the complexity of the causes and consequences of eco-evo feedback at the genome level.

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6 Author contributions

LM and AT prepared the initial draft, which was subsequently revised and improved by TS and DAA.

7 Conflict of interest

The authors do not declare any conflict of interest. The authors did not use any AI tools in the writing of this manuscript.

8 Data and Coding Availability statement

The code used to generate Figure 2 has been archived on GitHub: https://github.com/Luker121/life-history-traits-review-qpb.

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