INVITED REVIEWS AND SYNTHESES

Spatiotemporal landscape genetics: Investigating ecology and evolution through space and time

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Abstract

Genetic time-series data from historical samples greatly facilitate inference of past population dynamics and species evolution. Yet, although climate and landscape change are often touted as post-hoc explanations of biological change, our understanding of past climate and landscape change influences on evolutionary processes is severely hindered by the limited application of methods that directly relate environmental change to species dynamics through time. Increased integration of spatiotemporal environmental and genetic data will revolutionize the interpretation of environmental influences on past population processes and the quantification of recent anthropogenic impacts on species, and vastly improve prediction of species responses under future climate change scenarios, yielding widespread revelations across evolutionary biology, landscape ecology and conservation genetics. This review encourages greater use of spatiotemporal landscape genetic analyses that explicitly link landscape, climate and genetic data through time by providing an overview of analytical approaches for integrating historical genetic and environmental data in five key research areas: population genetic structure, demography, phylogeography, metapopulation connectivity and adaptation. We also include a tabular summary of key methodological information, suggest approaches for mitigating the particular difficulties in applying these techniques to ancient DNA and palaeoclimate data, and highlight areas for future methodological development.

KEYWORDS
ancient DNA, climate change, ecological genetics, genome–environment association, genotype–environment correlation, spatiotemporal population dynamics

1 | INTRODUCTION

By understanding how geographical features and climatic variance have historically shaped species genetic variability and population responses, we may be better able to meet conservation management goals for current and future climate challenges. To this end, genetic data from historical samples—i.e., ancient DNA (aDNA)—have revolutionized our ability to infer past population dynamics and species evolution (Slatkin & Racimo, 2016). While initial research tended to rely on the smaller and more prevalent mitochondrial genome (e.g.,

Higuchi, Bowman, Freiberger, Ryder, & Wilson, 1984; Pääbo, 1984), retrieval of nuclear genetic data is now regularly achievable, permitting the sequencing of entire ancient nuclear genomes (de Barros Damgaard et al., 2018; Meyer et al., 2012; Palkopoulou et al., 2015; Schlebusch et al., 2017). Furthermore, selective capture of regions of interest by hybridization of aDNA with oligonucleotide baits (Ávila-Arcos et al., 2011), combined with high-throughput sequencing, has led to the recent generation of unprecedented population-level genetic data sets (e.g., Haak et al., 2015; Lipson et al., 2017; Mathieson et al., 2015; Narasimhan et al., 2019).

The aDNA field is currently poised to fully leverage the genetic information stored in historical specimens to gain a better understanding of past **bioclimatic** drivers of evolutionary processes (Der Sarkissian et al., 2015). In fact, the greatest strength of ancient genetic data is that it provides a chronological genetic record of species' historical responses to environmental and anthropogenic change, including demographic bottlenecks and expansions (e.g., Niemi, Sajantila, Ahola, & Vilkki, 2018; Shapiro et al., 2004), population movements to track suitable habitat (e.g., Foote et al., 2013) and adaptive responses to selection pressures (e.g., Ludwig et al., 2015). Clearly, aDNA has the potential to profoundly inform questions of past species population dynamics in relation to environmental and anthropogenic perturbations. Several recent aDNA studies have begun addressing these types of questions, by noting the coincident timing of extinction events with contemporaneous climatic change (e.g., Lorenzen et al., 2011; Metcalf et al., 2016) or documenting selection through time (e.g., Librado et al., 2017; Mathieson et al., 2015). However, aDNA research in this regard still mostly lacks explicit connections among palaeoclimate, landscape and historical genetic data. Future advances in evolutionary biology will necessitate more integrated analysis methods.

In contrast, analyses in the field of landscape genetics explicitly integrate genetic and land cover or climate variables to determine the environmental factors that drive genetic variation and adaptation (Manel, Schwartz, Luikart, & Taberlet, 2003; Storfer, Patton, & Fraik, 2018). Landscape genetic studies utilize primarily modern genetic data to ascertain landscape and bioclimatic influences on population processes such as structure and connectivity (e.g., Berkman, Nielsen, Roy, & Heist, 2018; Stillfried et al., 2017), hybridization and introgression (e.g., Fitzpatrick & Shaffer, 2007; Geraldes et al., 2014), and the spatial variability in selection pressures (e.g., Poncet et al., 2010; Vincent, Dionne, Kent, Lien, & Bernatchez, 2013). Spatially explicit methods that integrate environmental and genetic data are therefore well established, and analytical techniques continue to advance (Rellstab, Gugerli, Eckert, Hancock, & Holderegger, 2015). Nevertheless, although some effort has been made recently to separate historical influences from contemporary patterns (Epps & Keyghobadi, 2015), the gains achieved in landscape genetics have rarely benefitted from the inclusion of temporal genetic data. Additional advances could be realized with a greater historical perspective. For instance, temporal samples and **heterochronous** analyses could inform numerous relevant landscape genetics questions, such as disentangling the role of human pressures from environmental change on population processes (Kidwell, 2015), understanding how anthropogenic impacts have affected genetic diversity and population connectivity through time (e.g., Pacioni et al., 2015), predicting how species will respond to proposed management actions or under different future climate change scenarios (e.g., Nogués-Bravo et al., 2016), or real-time genetic monitoring of selection (e.g., Hansen, Olivieri, Waller, & Nielsen, 2012).

Thus, there is broad scope for aDNA and landscape genetic research areas to come together and improve inference of temporal environmental and anthropogenic influences on species dynamics.

To that end, this review provides a summary of the latest analytical techniques for explicitly linking temporal landscape, climate and genetic data to assess spatiotemporal changes in five key research areas: population genetic structure, demography, phylogeography, metapopulation connectivity and adaptation. We additionally suggest approaches for mitigating the challenges in applying these techniques to aDNA and palaeoclimate data, and highlight areas for future methodological development in spatiotemporal landscape genetics.

2 | POPULATION GENETIC STRUCTURE

A firm knowledge of species' spatiotemporal population structure is crucial for accurate analysis and interpretation of many research questions in ecology and evolution. However, temporal population genetic structure is rarely considered in aDNA research (e.g., Shapiro et al., 2004), potentially resulting in misleading conclusions. Even when population structure is accounted for, "populations" are typically delineated based on predefined spatially or temporally proximate groups (e.g., Dalén et al., 2007; Ersmark et al., 2015; Pacioni et al., 2015). This is problematic because the assumed populations might not reflect the actual historical population genetic structure, which subsequently compromises downstream analyses. Moreover, ignoring population structure in temporal genetic studies is known to bias, mislead or otherwise obscure reconstructions of demographic changes through time (Chikhi et al., 2018; Chikhi, Sousa, Luisi, Goossens, & Beaumont, 2010; Heller, Chikhi, & Siegismund, 2013; Mazet, Rodríguez, & Chikhi, 2015; Mazet, Rodríguez, Grusea, Boitard, & Chikhi, 2016), and to produce highly inaccurate molecular dating results (Murray et al., 2016; Navascués & Emerson, 2009). Ignorance of population structure may also mask signatures of selection, especially if selection pressures are not consistent among subpopulations (Moeller, Tenaillon, & Tiffin, 2007), or result in false positive identification of loci under selection (François, Martins, Caye, & Schoville, 2016; Meirmans, 2012). Thus, although assessing species' population genetic structure through time does not necessitate linking climate and land cover data, temporal changes in species population structure are often the result of landscape and environmental change, and this information is crucial to understanding a species' history and future conservation. We therefore briefly introduce the topic of spatiotemporal population genetic structure here and direct interested readers to a more detailed treatment of potential analysis methods in the supplementary Appendix.

Numerous approaches have been developed to describe the underlying population structure from a set of genetic samples and have been applied to heterochronous samples to varying degrees (Table 1; Supplementary Appendix). Clustering algorithms such as STRUCTURE (Pritchard, Stephens, & Donnelly, 2000) or ADMIXTURE (Alexander & Lange, 2011; Alexander, Novembre, & Lange, 2009) group samples based on an underlying genetic model, which eliminates the need for defining populations at the outset (Pritchard et al., 2000). Several model-based methods for assessing population genetic structure

are also spatially explicit (e.g., Baps, Corander, Sirén, & Arjas, 2008; Geneland, Guillot, Mortier, & Estoup, 2005, Guillot, Renaud, Ledevin, Michaux, & Claude, 2012; Tess, Chen, Durand, Forbes, & François, 2007; Caye, Deist, Martins, Michel, & François, 2016), meaning they can incorporate the sampling locations of individuals to strengthen the cluster inference based on spatial **autocorrelation** of allele frequencies.

Although these model-based clustering techniques are powerful methods for naively inferring species population structure history, model-based approaches may not be entirely appropriate for temporal data sets, as the assumptions of the underlying genetic models (i.e., Hardy–Weinberg equilibrium and minimal linkage disequilibrium) will be violated when samples are many generations apart. Nonetheless, this may be a desirable feature because these algorithms can identify temporal structure as well. By minimizing a temporal Wahlund effect, clustering methods could be used to investigate population stability or turnover through time (e.g., Nyström et al., 2012; Xenikoudakis et al., 2015).

As an alternative to model-based clustering techniques, model-free methods do not make assumptions regarding underlying genetic models and generally have faster computation times for genome-scale data. Most model-free approaches are ordination analyses like principal components analysis (PCA; Hotelling, 1933; Pearson, 1901) or principal coordinates analysis (PCoA; Torgerson, 1952) that reduce multivariate data into orthogonal dimensions that maximize the variance among the measurements. Several model-free methods are also spatially explicit (e.g., spatial PCA [sPCA], Jombart, Devillard, Dufour, & Pontier, 2008; spatial factor analysis [spFA], Frichot, Schoville, Bouchard, & François, 2012), which may improve the inference and interpretation of population genetic structure by incorporating geographical sample locations.

Although ordination methods are useful for visualizing patterns in complex data, a priori group definitions are typically required to assess clustering patterns and there are limited (or nonexistent) options for determining the significance of clustering. Still, approaches to naively cluster individuals do exist (such as *k*-means clustering; Steinhaus, 1956; MacQueen, 1967; see also Jain, 2010), although they have rarely been used in this context (but see e.g., Jombart, Devillard, & Balloux, 2010). Other approaches based on network theory (e.g., PopGraph, Dyer, 2014; NetStruct, Greenbaum, Templeton, & Bar-David, 2016) do not rely on a genetic model per se, but cluster individuals naively based on measures of genetic relatedness, and also provide a means for assessing the significance of the clustering signal.

While several approaches for assessing population genetic structure are spatially explicit, few techniques are temporally explicit. Most methods are unable to control for temporal autocorrelation (but see spatiotemporal PCA [stPCA] applications, e.g., Gallacher et al., 2017; Stahlschmidt, Härdle, & Thome, 2015), and only one approach directly incorporates the effects of genetic drift through time (Dystruct; Joseph & Pe'er, 2018). Indeed, most current population genetic structure analyses were designed to evaluate samples collected from a single snapshot in time, and as

such may be biased when confronted with samples encompassing hundreds or thousands of generations. However, although it is not yet clear which analysis methods are best suited for heterochronous data (especially with opportunistically collected samples from widely disparate locations and time periods), applying a combination of approaches will undoubtedly provide important insight into species' spatiotemporal population structure and critically inform downstream analyses of, for example, demography and adaptation.

3 | DEMOGRAPHY

Demographic studies evaluate changes in population size over time and a key question in demographic research is to understand what factors precipitated those population fluctuations. Yet, while climate change or anthropogenic factors are frequently cited as causal drivers (e.g., Johnson et al., 2016; Saltré et al., 2016; Shapiro et al., 2004), these associations are generally assumed based solely on the coincident timing of large climate (or anthropogenic) shifts with subsequent population size change (e.g., Prost et al., 2010) or species replacements (e.g., Soubrier et al., 2016). Causal inferences would be much stronger with more integrated analysis methods and hypothesis testing of proposed driving factors relative to temporal changes in population size. To that end, we discuss below several analytical approaches that meet these objectives.

3.1 | Landscape-informed demographic modelling

When identifying factors that may have influenced species demographic changes, a general approach is to model changes in the proposed driving factors through time (habitat availability, climate variables, human population size, etc.) and evaluate how well changes in those factors correlate with observed changes in population size for the target species. Approximate Bayesian computation (ABC) is a flexible statistical framework that can be applied to wide-ranging research questions, including the inference of environmental and anthropogenic drivers of demographic change (reviewed by Bertorelle, Benazzo, & Mona, 2010). ABC simulations can explicitly incorporate heterochronous samples, as well as spatial heterogeneity and temporal environmental fluctuations (Table 1). Briefly, the user begins by describing the demographic models to be tested, which may include any number of hypothesized demographic events such as population bottlenecks, expansions, extinctions, migrations or size changes. The timings of these events can be specified if known or included as one of the parameters to be estimated. A multitude of demographic and ecological parameters can also be considered with ABC, such as mutation rates, migration rates and carrying capacity. Once the prior distributions of the parameters are defined, simulations of all models and parameter space are performed. Summary statistics are used to compare the simulated models with the observed data and the use of spatially explicit summary statistics may improve the ability

TABLE 1 Features of analysis techniques for associating spatiotemporal genetic, landscape and climate data

Research area	Example analysis methods[a]	Suitable genetic markers[b]	Accommodation of missing genetic data?[c]	Incorporation of heterochronous data?[d]	Analysis notes	Example applications to spatiotemporal genetic and/or environmental data
Population structure	**Clustering** STRUCTURE (Pritchard et al., 2000); FRAPPE (Tang, Peng, Wang, & Risch, 2005); ADMIXTURE (Alexander & Lange, 2011; Alexander et al., 2009); FASTSTRUCTURE (Raj, Stephens, & Pritchard, 2014)	STR, SNP	Yes	G	See Note 1	Mondol, Bruford, and Ramakrishnan (2013); Raghavan et al. (2015); Frisch et al. (2017)
	DYSTRUCT (Joseph & Pe'er, 2018)	SNP	Yes	G		
	Spatially explicit clustering GENELAND (Guillot et al., 2005, 2012)	Sequence, STR, SNP	Yes	G	See Note 1	Cousseau, Husemann, Foppen, Vangestel, and Lens (2016); Baudouin et al. (2017)
	TESS (Caye et al., 2016; Chen et al., 2007)	STR, SNP	Yes	G	See Note 1	Martin et al. (2014)
	BAPS (Cheng, Connor, Sirén, Aanensen, & Corander, 2013; Corander et al., 2008; Corander, Waldmann, & Sillanpaa, 2003)	Sequence, STR, SNP	Yes	G	See Note 1	Orsini, Corander, Alasentie, and Hanski (2008); Chu et al. (2014)
	Model-free PCA—SMARTPCA (Patterson, Price, & Reich, 2006; Price et al., 2006); R package ADEGENET (Jombart, 2008; Jombart & Ahmed, 2011); R package LEA (Frichot & François, 2015)	Sequence, STR, SNP	No	G	See Notes 2, 3, 4	Skoglund et al. (2012); Spurgin et al. (2014); Raghavan et al. (2015);
	PCoA—R package APE (Paradis, Claude, & Strimmer, 2004; Paradis, Schliep, & Schwartz, 2018)	Sequence, STR, SNP	No	G	See Notes 3, 5	Xenikoudakis et al. (2015)
	Spatially explicit model-free sPCA—R package ADEGENET (Jombart, 2008; Jombart & Ahmed, 2011)	Sequence, STR, SNP	No	G	See Notes 2, 3, 4	Holmes (2014)
	spFA—R script available at http://membres-timc.imag.fr/Olivier.Francois/spfa.R	Sequence, STR, SNP	No	G	See Notes 2, 3, 4	
	stPCA—R script available at http://researchdata.gla.ac.uk/277/	Sequence, STR, SNP	No	G	See Notes 2, 3, 4	
	Naïve clustering model-free DAPC—R package ADEGENET (Jombart; Jombart & Ahmed, 2011)	Sequence, STR, SNP	No	G	See Notes 2, 3, 4	Jombart et al. (2010); Prost et al. (2013); Therkildsen et al. (2013)
	Network theory clustering—PoPGRAPH (Dyer & Nason, 2004); NETSTRUCT (Greenbaum et al., 2016)	STR, SNP	Yes	G		

TABLE 1 (Continued)

Research area	Example analysis methods[a]	Suitable genetic markers[b]	Accommodation of missing genetic data?[c]	Incorporation of heterochronous data?[d]	Analysis notes	Example applications to spatiotemporal genetic and/or environmental data
Demography	Landscape-informed demographic modelling	ABC—SPLATCHE (Currat, Ray, & Excoffier, 2004; Ray, Currat, Foll, & Excoffier, 2010); AQUASPLATCHE (Neuenschwander, 2006)	Sequence, STR, SNP	Yes	E	See Note 6	Eriksson et al. (2012)
		ABC—BAYESIAN SERIAL SIMCOAL (Anderson, Ramakrishnan, Chan, & Hadly, 2005; Excoffier, Novembre, & Schneider, 2000), available at https://web.stanford.edu/group/hadlylab/ssc/; FASTSIMCOAL (Excoffier & Foll, 2011)	Sequence, STR, SNP	Yes	G	See Note 6	Alter, Newsome, and Palumbi (2012)
		ABC—ABCTOOLBOX (Wegmann, Leuenberger, Neuenschwander, & Excoffier, 2010)	Sequence, STR, SNP	Yes	G, E	See Notes 6, 7	Raghavan et al. (2015)
		(Carrying Capacity) SDMs—MAXENT (Phillips & Dudík, 2008); GARP (Stockwell & Noble, 1992); BIOENSEMBLES (Diniz-Filho et al., 2009)	NA	NA	E	See Note 8	Hung et al. (2014); Prates et al. (2016)
	Predictive Correlations	CCM—R package rEDM (Ye, Clark, Deyle, & Sugihara, 2016)	Sequence, STR, SNP	Yes	G, E	See Note 9	Deyle et al. (2013); Cramer, O'Dea, Clark, Zhao, and Norris (2017)
Phylogeography	Lineage range evolution	Ancestral Range Dynamics—LAGRANGE (Ree & Smith, 2008); R package BIOGEOBEARS (Matzke, 2014); LAGRANGE C++ (Reddy & Condamine, 2016)	Sequence, STR, SNP	Yes	G, E	See Notes 10, 11	Mitchell et al. (2014); Tseng et al. (2014); Fabre et al. (2016); Marki et al. (2017)
		Spatial Lineage Diffusion—BEAST 1.10 (Suchard et al., 2018)	Sequence, STR, SNP	Yes	G		Barnett et al. (2014)
		SDM-ABC applications (see SDM and ABC notes above)	Sequence, STR, SNP	Yes	G, E		Chan et al. (2011); Hope et al. (2015)
	Environmental correlates of lineage dispersal	SERAPHIM (Dellicour, Rose, Faria, et al., 2016)	Sequence, STR, SNP	Yes	G	See Note 10	Dellicour, Rose, and Pybus (2016); Jacquot, Nomikou, Palmarini, Mertens, and Biek (2017)
Metapopulation connectivity	Population migrations through time	SDM-Connectivity (see also SDM notes above) –SDMTOOLBOX (Brown, 2014); CIRCUITSCAPE (McRae & Shah, 2009); GFLOW (Leonard et al., 2017)	Sequence, STR, SNP	Yes	G, E	See Note 12	Wasserman et al. (2012); Dupas et al. (2014); Fant, Havens, Keller, Radosavljevic, and Yates (2014); Razgour (2015); Yu et al. (2017)

(Continues)

TABLE 1 (Continued)

Research area	Example analysis methods[a]	Suitable genetic markers[b]	Accommodation of missing genetic data?[c]	Incorporation of heterochronous data?[d]	Analysis notes	Example applications to spatiotemporal genetic and/or environmental data
	Ancestry Distribution Models—Pops (Jay et al., 2015)	STR, SNP	Yes	E		Temunović, Frascaria-Lacoste, Franjić, Satović, and Fernández-Manjarrés (2013)
Spatiotemporal population connectivity	Graph Theory—R package GSTUDIO (Dyer, 2012)	Sequence, STR, SNP	Yes	G, E	See Note 12	See Draheim, Moore, Fortin, and Scribner (2018) for a related approach.
	Gravity Models—R package GeNetIt (Evans & Murphy, 2017)	Sequence, STR, SNP	Yes	G, E	See Note 12	See Draheim, Moore, Fortin, and Scribner (2018) for a related approach.
Adaptation	MatSAM (Joost et al., 2008); SamβADA (Stucki et al., 2017)	STR, SNP	Yes	G, E	See Note 13	Frisch et al. (2017)
Logistic regressions	R package GEEPACK (Halekoh, Højsgaard, & Yan, 2006)	STR, SNP	Yes	G, E	See Note 13	
Linear regressions	BAYENV (Coop et al., 2010); BAYENV2 (Günther & Coop, 2013)	STR, SNP	Yes	G, E	See Note 13	van Heerwaarden et al. (2012); Therkildsen et al. (2013)
	SPATPG (Gompert, 2016)	STR, SNP	Yes	G, E		
Linear mixed models	GINLAND (Guillot et al., 2014)	STR, SNP	Yes	G, E	See Notes 13, 14	
Ordination-based regressions	LFMM (Frichot et al., 2013); R package LEA (Frichot & François, 2015)	STR, SNP	Yes	G, E	See Notes 13, 15	
	R package VEGAN (Oksanen et al., 2017); R package PCADAPT (Luu, Bazin, & Blum, 2017)	STR, SNP	No	G, E	See Notes 13, 16	Frisch et al. (2017)
F_{ST}-based genome scan with environment	BAYESCENV (Villemereuil & Gaggiotti, 2015)	STR, SNP	Yes	G, E	See Notes 13, 17	
Nonlinear associations	R package GDM (Manion, Lisk, Ferrier, Nieto-Lugilde, & Fitzpatrick, 2018)	Sequence, STR, SNP	No	G, E	See Notes 5, 13	Fitzpatrick and Keller (2015)
	R package GRADIENTFOREST (Ellis et al., 2012)	Sequence, STR, SNP	No	G, E	See Notes 2, 13	Fitzpatrick and Keller (2015); Bay et al. (2018)

Abbreviations: ABC, approximate Bayesian computation; CCA, canonical correspondence analysis; CCM, convergent cross mapping; DAPC, discriminant analysis of principal components; dbRDA, distance-based redundancy analysis; GDM, generalized dissimilarity model; GF, gradient forest; LFMM, latent factor mixed models; NA, not applicable; PCA, principal components analysis; PCoA, principal coordinates analysis; RDA, redundancy analysis; SDM, species distribution model; sPCA, spatial principal components analysis; spFA, spatial factorial analysis; stPCA, spatio-temporal principal components analysis.

Analysis footnotes:

[1]Although technically there is no impediment to applying these analyses to heterochronous samples, the models assume a contemporaneous population.

TABLE 1 (Continued)

[2]Sequence data such as mitochondrial genomes can be analysed as haplotype frequencies.

[3]Missing data points must either be discarded or imputed.

[4]Although technically there is no impediment to applying PCA to heterochronous samples, Duforet-Frebourg and Slatkin (2016) identified systematic biases in PCA related to the age of the sample. It is expected that a similar bias would exist for the PCA-derivative analysis methods as well, although this has not been formally tested.

[5]The choice of molecular marker is only constrained by the use of an appropriate genetic distance that can be constrained between 0 and 1. Sequence data can be used with an appropriate genetic distance such as a rescaled haplotype network distance.

[6]ABC analyses rely on the comparison of summary statistics between the observed and simulated data. Thus, the method's ability to accommodate missing genetic data depends on the summary statistics used.

[7]To our knowledge, there is no single program to conduct demographic simulations that can incorporate both heterochronous samples and spatiotemporal landscape heterogeneity. However, ABCтооlвох can integrate other simulators such as those listed above, facilitating comparisons of demographic models that incorporate heterochronous genetic or environmental data.

[8]Estimating demographic history based on temporal habitat availability does not require genetic information, only dated fossil records—but see Gotelli and Stanton-Geddes (2015) for approaches to integrate the data types. However, carrying capacity SDMs are typically used as independent verification of the role of environmental change on genetically derived estimates of demographic history.

[9]CCM analyses utilize time series population size estimates and environmental data. Thus, determining suitable genetic markers and the method's ability to accommodate missing genetic data depends on the demographic method used to estimate population sizes through time.

[10]Suitable molecular markers and accommodation of missing genetic data are constrained only by the method used to create the spatiotemporally referenced phylogenetic tree.

[11]Temporal changes in habitat availability can be used to temporally constrain dispersal events among areas.

[12]Pairwise genetic information is generally used to define the connectivity network, to inform the development of landscape resistance surfaces, or to test the likelihood of different routes. Suitable molecular markers and accommodation of missing genetic data are constrained only by the method used to calculate an appropriate pairwise genetic distance metric, migration rates or shared haplotype network.

[13]With this method, individuals or populations can be associated to their respective temporally-relevant environment values. However, it may be important to conduct additional outlier tests and determine the age of selected alleles. If the sample set spans large fluctuations in selection strength for example, it may be necessary to conduct time–slice analyses to accurately determine genotype–environment relationships.

[14]Because this approach is spatially explicit, it may be more appropriate to conduct time–slice analyses to better accommodate changing environmental conditions occurring at the same locations.

[15]While the program can technically handle missing data, missing data will bias the significance tests. The authors recommend imputation and the r package LEA has a basic imputation algorithm; however, users should also be aware of the potential biases of imputation and analysing incomplete data sets.

[16]Alternatively can perform a partial ordination analysis and partial out the effect of time.

[17]Because BAYESCENV relies on environmental differences to a reference value, it would also be possible to standardize the environmental variables relative to a given point in time.

[a]Only a subset of potential analysis programs is listed here; additional software may be available for some analyses.

[b]Sequence = DNA sequence data, such as Y-chromosome or mitochondrial D-loop sequences or chloroplast genomes; STR = short tandem repeat; SNP = single nucleotide polymorphism. This column lists only whether the programs mentioned can utilize STR, SNP or sequence data as input; programs may be able to incorporate other marker types (such as amplified fragment length polymorphism) as well. Users should be aware of the implications of different marker choices on analysis and interpretation.

[c]This column lists only whether the analysis or programs mentioned can handle any missing genetic data (e.g., several missing loci per individual or incomplete sequences). Users should be aware of important biases that may result when attempting to analyse samples with missing data.

[d]E = method can directly utilize heterochronous environmental data (as opposed to necessitating a time–slice approach); G = method can directly utilize heterochronous samples or genetic data.

to discriminate among alternative evolutionary scenarios with similar genetic signatures (Alvarado-Serrano & Hickerson, 2016). Finally, the model and parameters that best match the observed data are considered the most likely scenarios of the species history. As a hybrid analysis between statistical inference and simulations, ABC can thus improve interpretations of the historical bioclimatic processes that have influenced species demography through time.

An extension of the ABC technique is to construct species distribution models (SDMs) of habitat occupancy through time to generate hypotheses regarding historical population processes, which can then be tested with genetic data. SDMs are correlative models that associate known species presence (and absence, if known) data with various bioclimatic variables (reviewed by Araújo & Peterson, 2012). These associations are then used to predict the likelihood of a species presence at different locations or time periods based on the projected distribution of that species' environmental associations. These models assume niche conservatism through time, but with the use of aDNA and fossil localities, environmental associations can be temporally modified if necessary to reflect more accurate historical use patterns (Nogués-Bravo, 2009). SDMs and ABC models have been used to test hypotheses concerning drivers of bison demographic change through time (Metcalf et al., 2014). Dated fossil localities were used to define the occupied bioclimatic niche and predict suitable bison habitat distribution for five historical time periods, to estimate potential temporal changes in population structure. The proposed population structures were combined with hypothesized influences of anthropogenic hunting (both Native American subsistence hunting and overexploitation following European settlement scenarios) on population size to develop multiple demographic models. The likelihood of the models was then tested with ABC, using temporal genetic data from ancient specimens. The models with the greatest support favoured a demographic history in which bison comprised a single cohesive population in the late Holocene. The best-ranked model also included the deleterious effects of widespread hunting following European settlement—a known dramatic population bottleneck that nearly drove the species to extinction.

A novel application of SDMs to assess demography is to use them to estimate the carrying capacity of the landscape at a given time. This approach not only predicts temporal changes in the spatial distribution of a species, but also provides an estimate of population size change based on habitat quality and availability (Figure 1). This technique was used to model demographic change in the American pika (*Ochotona princeps*) since the last glacial maximum (LGM; Brown & Knowles, 2012). SDMs of habitat suitability were created for 500-year **intervals** and transformed into estimates of the number of individuals each landscape could support. Dispersal probability was also modelled from the SDMs such that highly suitable habitat would have the lowest dispersal cost and vice versa. Spatially explicit ABC simulations were then used to model population change and migration through time based on the changes in the landscape. The carrying capacity landscapes resulted in estimates of population size changes through time that coincided well with independent genetic
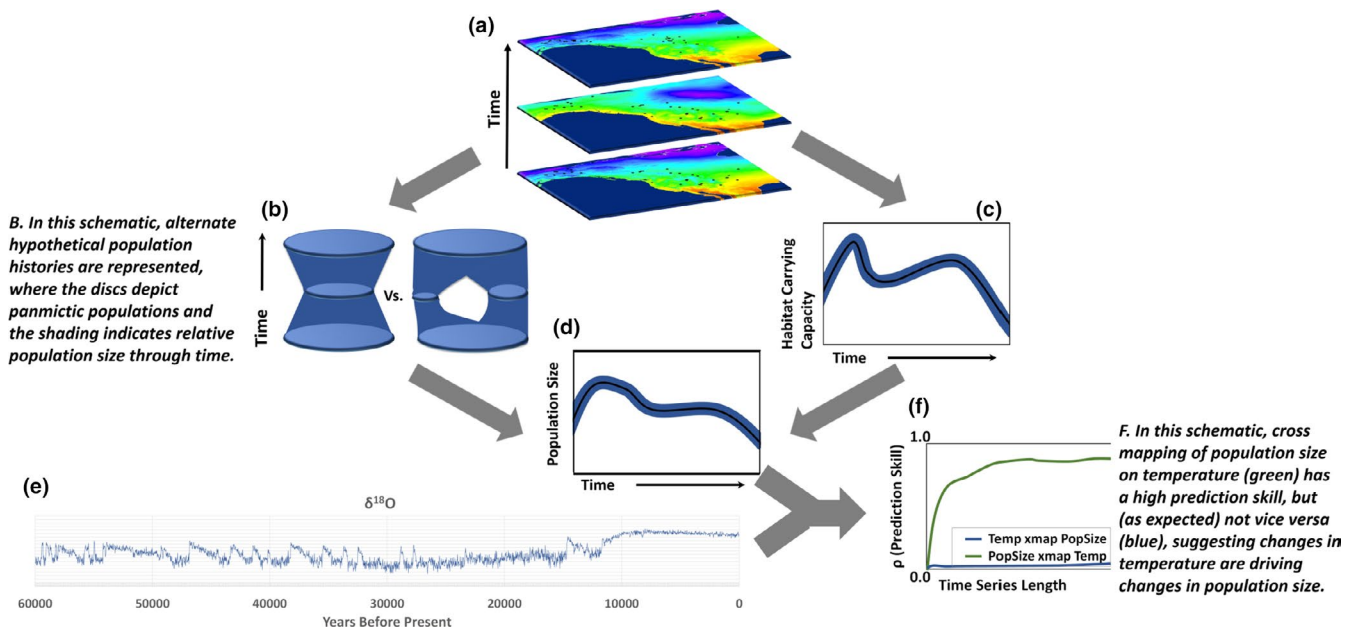

FIGURE 1 Approaches for investigating the influence of environmental change on demography over time. Spatial models of land cover or bioclimatic change through time (a) can be used to estimate temporal changes in habitat quality and availability to generate alternative demographic hypotheses that can be evaluated with approximate Bayesian computation (b) or to infer spatiotemporal habitat carrying capacity as a proxy for the species maximum population size through time due to ecological constraints (c). The validity of these models is then evaluated by comparison to the observed genetic data and coalescent estimates of temporal demographic patterns (d). Alternatively, the driving influence of time series bioclimatic variables such as temperature proxies (e) on population fluctuations can be tested with predictive convergent cross mapping models (f). Data shown in (a) are from Hijmans, Cameron, Parra, Jones, and Jarvis (2005) and in (e) from Svensson et al. (2008)

Bayesian skyline-plot demographic estimates, supporting a habitat-driven population decline for pikas since the LGM. Thus, dynamic SDM carrying capacity models can provide independent support of the impact of environmental change on population sizes.

3.2 | Predictive correlations

Dynamic time series models are also highly suitable for directly inferring drivers of demographic change. Granger causality (Granger, 1969; Wiener, 1956) is a statistical concept that determines whether one time series variable impacts another by calculating if changes in variable Y can be better predicted from past values of variable X and Y, over and above what can be predicted from past values of Y alone. Thus, methods based on Granger causality use prediction rather than correlation to make inferences about cause-and-effect relationships. However, a key requisite of Granger causality tests is that putative causal factors are completely independent from the effect variable, which may not always be the case in ecological systems. For example, in deterministic dynamic systems such as boom–bust predator–prey population cycles, information about the driving variable X (e.g., prey population size) is also echoed in the effect variable Y (e.g., predator population size).

One approach that has been developed to overcome the above issue of dependence is convergent cross mapping (CCM; Sugihara et al., 2012). In contrast to Granger causality, CCM assesses causation by evaluating how well past values of Y can predict X, which would only occur if changes in X drive changes in Y. Essentially, CCM seeks the redundant echo of X in the time series of Y. This technique can be used to detect both unidirectional and bidirectional cause-and-effect relationships. The relative strength of the cross-map correlations between two bidirectionally coupled variables can also provide insight into which is the driving variable (Figure 1). Additionally, it is also possible to estimate the **lag** time between changes in driving factors and the effects on species demography, as well as more complex relationships such as external forcing of unlinked variables and indirect causal relationships (Ye, Deyle, Gilarranz, & Sugihara, 2015).

To demonstrate the utility of CCM for discerning drivers of demographic change through time, Sugihara et al. (2012) applied it to two well-studied systems. The first was a predator–prey relationship between the protist genera *Didinium* (predator) and *Paramecium* (prey). Under laboratory conditions, they monitored the abundance
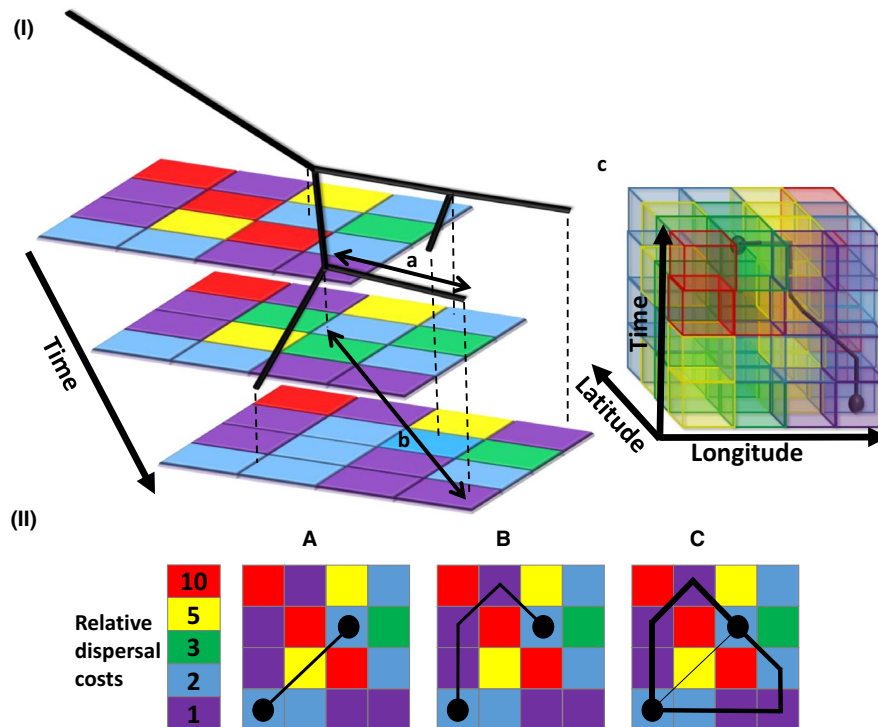

FIGURE 2 Testing the influence of environmental factors on lineage dispersal. (I) The spatiotemporal distance of each phylogenetic branch of a distance-based phylogeny (a) is correlated with the effective geographical distance (EGD) of that branch (b). EGDs are estimates of lineage dispersal costs based on the underlying landscape model and selected path model, which in a spatiotemporal context would be a "3D" distance (i.e., a **space-time path** (c); Hägerstraand, 1970) through a three-dimensional landscape (i.e., a **space-time cube**) to incorporate changes in the landscape through time. (II) Example path models (shown in two dimensions for clarity): Euclidean distance (A) is the shortest (spatiotemporal) straight-line distance between two points. Least-cost paths (B) and circuit paths (C) require a (3D) model of the landscape with each feature classified according to its hypothesized influence on dispersal success. The least-cost path is the single path that minimizes the total cumulative cost of dispersal. Circuit paths are modelled like circuit boards, where the amount of current (i.e., likelihood of lineage dispersal) between two nodes is a function of the resistance along the path. Thus, multiple paths can be identified, and their relative widths are hypothesized to be correlated with the likelihood of lineage dispersal along that route

oscillations of the two species through time and revealed with CCM that the population sizes of the two species were causally linked. Moreover, the cross-map skill of *Didinium* abundance from the *Paramecium* time-series data was greater than for the reverse, suggesting a top-down system where the predator population cycles were driving the prey population dynamics. The second example included annual California fishery landings of anchovy and sardines (as a proxy for species abundance through time), and annual sea surface temperatures. In this system, sardines tend to be abundant when anchovy populations are low and vice versa, suggesting competitive exclusion may be a driving factor in population size for the two species. The application of CCM demonstrated that there was no interaction between sardines and anchovies, but that the populations of both species were weakly impacted by sea surface temperature. Thus, methods like these that directly link temporal genetic and environmental data can be applied to help resolve numerous evolutionary demographic questions, from identifying the driving climate factors that have significantly impacted species through time, to evaluating community dynamics or the impact of biotic invasions by assessing the interaction of species demographic histories.

4 | PHYLOGEOGRAPHY

Determining a species phylogeographical history can greatly inform knowledge of historical migration events and evolution (Knowles, 2009). For instance, georeferenced and dated phylogenies can be used to hypothesize the biogeographical causes of speciation events or population histories (e.g., Baker, Huynen, Haddrath, Millar, & Lambert, 2005; Heintzman et al., 2016). However, most phylogeographical analyses remain descriptive in nature, because patterns are primarily determined by post-hoc mapping of spatiotemporally referenced haplotypes (e.g., Bray et al., 2013; Larson et al., 2007) and analyses do not incorporate climate or landscape variables directly. Thus, highlighted here are spatiotemporal analyses that may better elucidate the effects of landscape and climate processes on species evolutionary history.

4.1 | Lineage range evolution

Understanding how phylogenetic lineages colonized different geographical regions and the timing of those dispersals are key motivations of phylogeographical research. Several approaches are available for discerning spatiotemporal dynamics and historical dispersal pathways of phylogenetic lineages. For instance, biogeographical methods have been developed that utilize phylogenetic information to better infer ancestral species range dynamics (for a review see Ronquist & Sanmartín, 2011). Maximum-likelihood inference can be used to model range evolution while accounting for dispersal, local extinction and clade generation through time (Ree & Smith, 2008). This modelling framework can incorporate numerous types of spatiotemporal data to inform the results, such as range

dispersal constraints based on fossil localities, and environmental data such as palaeoclimate and tectonic records. Recent extensions can integrate more complex range dynamics, such as founder events (Matzke, 2014) and partial range shifts (Reddy & Condamine, 2016). This phylogeographical approach was used to infer the geographical origin and ancestral ranges of large felid species, as well as to identify lineage dispersal events (Tseng et al., 2014).

As an alternative means for evaluating lineage dispersal, Edwards et al. (2011) applied a spatially explicit phylogeographical model to evaluate the spatial dynamics of polar bear (*Ursus maritimus*) and brown bear (*U. arctos*) matrilineages through time. An extension of a method originally developed for tracking the dispersion of evolving contagions (Lemey, Rambaut, Drummond, & Suchard, 2009), this Bayesian technique uses dated phylogenies to infer the spatial diffusion of lineages between locations. The method estimates dated asymmetric dispersal rates between pairs of locations to infer broad-scale, lineage-specific, spatiotemporal migration histories. In this case, Edwards et al. (2011) found a significant maternal dispersal pathway from Britain and Ireland for the polar bear lineage, suggesting modern polar bears may have arisen from the British Isles. Their results further pointed to brown bear matrilines diffusing from Alaska throughout eastern Siberia, Japan, and central and eastern Europe, which was attributed to rapid, long-distance dispersal events from Ice Age refugia.

SDMs have also been applied in various capacities to evaluate the impacts of climate change on species phylogeography (Alvarado-Serrano & Knowles, 2014). For example, to investigate the phylogeography of the hourglass treefrog (*Dendropsophis ebraccatus*), Chan, Brown, and Yoder (2011) developed SDMs for four time periods (present, mid-Holocene, LGM and last interglacial). By overlaying models of habitat suitability for these four significantly different climate periods, areas that remained consistently suitable were presumed to represent locations of relative ecological stability and act as potential refugia for the treefrog through time. From these putative refuge locations, several possible phylogeographical recolonization scenarios were proposed that were then tested with the genetic data in an ABC framework. By including historical phylogeographical responses, the accuracy of range shift predictions for extant species under future climate change scenarios can also be improved (Fordham, Brook, Moritz, & Nogués-Bravo, 2014).

4.2 | Environmental correlates of lineage dispersal

Explicit assimilation of dated phylogenies and bioclimatic data is further realized with the R (R Core Team, 2016) package SERAPHIM (Dellicour, Rose, Faria, Lemey, & Pybus, 2016). These tools statistically evaluate the influence of environmental variables on lineage dispersal. The SERAPHIM analysis requires a phylogeny where each tip and internal node are georeferenced and dated, although some of these parameters can be estimated (e.g., Lemey, Rambaut, Welch, & Suchard, 2010). The trajectory of each phylogenetic branch is

calculated with a vector incorporating the spatial and temporal distance between the start and end points of the branch (Figure 2). Effective geographical distances along each phylogenetic branch are calculated from underlying landscape models for each environmental variable of interest. Models with the strongest phylogenetic and environmental correlations indicate the landscape variables presumed to have had the greatest influence facilitating or restricting lineage spread. Although the method is designed for univariate environmental predictors, more complex multivariate landscapes could also be tested (e.g., Amaral, Palace, O'Brien, Fenderson, & Kovach, 2016). Dellicour, Rose, and Pybus (2016) applied SERAPHIM to reveal landscape influences on the temporal spread of the rabies virus in raccoons in the eastern United States over the past 30 years. Higher elevations were found to significantly hinder the spread of rabies in raccoons, which supports earlier work that suggested mountain ranges pose a probable dispersal impediment for the host species.

Because SERAPHIM was designed with rapidly evolving pathogens in mind, the primary limitation to its applicability in other species is the inability of the analysis to also accommodate evolving landscapes. Conceivably, the approach could still be applied to phylogenetic **time slices** of more slowly evolving organisms, depending on the scale of palaeoclimate data available. In this manner, it may be possible to infer whether environmental influences on lineage dispersal have remained constant through time, or if ecological factors have driven diversification among different clades.

5 | METAPOPULATION CONNECTIVITY

Understanding connectivity among populations and how it changes through time is critical for revealing key population processes and evolutionary patterns (Lindenmayer, Hobbs, & Montague-Drake, 2008). Significant changes in connectivity can lead to population isolation or hybridization (Frankham, Ballou, & Briscoe, 2002; Keyghobadi, 2007), and thus recognizing temporal fluctuations in connectivity can crucially inform the phylogeographical history and conservation management of a species. Connectivity analyses can be used as a tool to reveal the effects of environmental variables on species dispersal, test the role of climate change on speciation or hybridization, identify historical migration corridors and determine the key climate factors with the greatest influence on species distributions. Yet, few studies to date have addressed changes in connectivity with heterochronous samples. Metapopulation connectivity has, on the other hand, been extensively explored using contemporaneous genetic samples in conjunction with heterochronous environmental data, and several of these approaches (discussed below) may be extensible to temporal genetic samples as well.

5.1 | Population migrations through time

One avenue for investigating the role of climate and landcover change on metapopulation dynamics is the identification of connectivity and/or population migration corridors through space and time, based on environmental suitability. One tool amenable to these research objectives are SDM-connectivity approaches, which relate connectivity and gene flow among populations to habitat suitability through time (e.g., Wasserman, Cushman, Shirk, Landguth, & Littell, 2012). For example, using this approach, putative dispersal routes for the Himalayan hemlock (*Tsuga dumosa*) were identified as the species recolonized from glacial refugia during the Quaternary period (Yu et al., 2015). To achieve this, SDMs were developed for three Quaternary time periods to identify areas of stable hemlock habitat suitability, as well as areas of probable range contraction and expansion between the time periods studied. Using a least-cost paths approach (see Figure 2) between shared haplotypes, probable pathways of dispersal and connectivity during each investigated time period were also identified.

A drawback of the above example is the assumption that contemporary patterns of shared haplotypes can describe connectivity patterns across highly disparate timescales. Although the different marker types used in the study (i.e., mitochondrial, chloroplast and nuclear haplotypes) are informative at different timescales (Wang, 2010), the inclusion of dated aDNA samples would vastly improve the inferences gained. By including historical samples, more accurate time-slice estimates of connectivity patterns can be achieved by virtue of analysing samples from the actual time periods considered, and that are thus relevant to the temporal resolution of the genetic markers used.

In another SDM-connectivity application, landscape connectivity models were used to describe plausible future distributions of the grey long-eared bat (*Plecotus austriacus*) in the face of climate change (Razgour, 2015). SDMs were created for current habitat suitability, as well as habitat projected to the year 2070 under an assumed climate change scenario. Relevant variables predicted from the habitat suitability analysis were further modelled to estimate landscape connectivity among patches based on circuit theory (see Figure 2; McRae, 2006). Once the landscape variables that influenced connectivity in the grey long-eared bat were identified, SDM analysis of future habitat suitability was used to predict future range shift pathways. The majority of the southern Iberian Peninsula was predicted to be unsuitable for grey long-eared bats by 2070 and several corridors were identified that may provide connectivity through time to accommodate a range shift to northern refugia.

Similar SDM-connectivity approaches could also be used to investigate historical connectivity. The relative influences of different environmental variables for facilitating or hindering migration at different time periods could be assessed by correlating relevant genetic distances with effective geographical distances on hypothesized cost surfaces (Spear, Cushman, & McRae, 2016), using samples from each time period. Landscape resistance maps could then be developed for multiple time periods to estimate historical range shift pathways or major migration routes during historical climate shifts. By forecasting range shift pathways from a historical time period, and hindcasting range shift pathways from a more recent time period, paths identified in common may indicate the most probable historical migration routes.

BOX 1 Properties of a hypothetical spatiotemporal landscape connectivity network
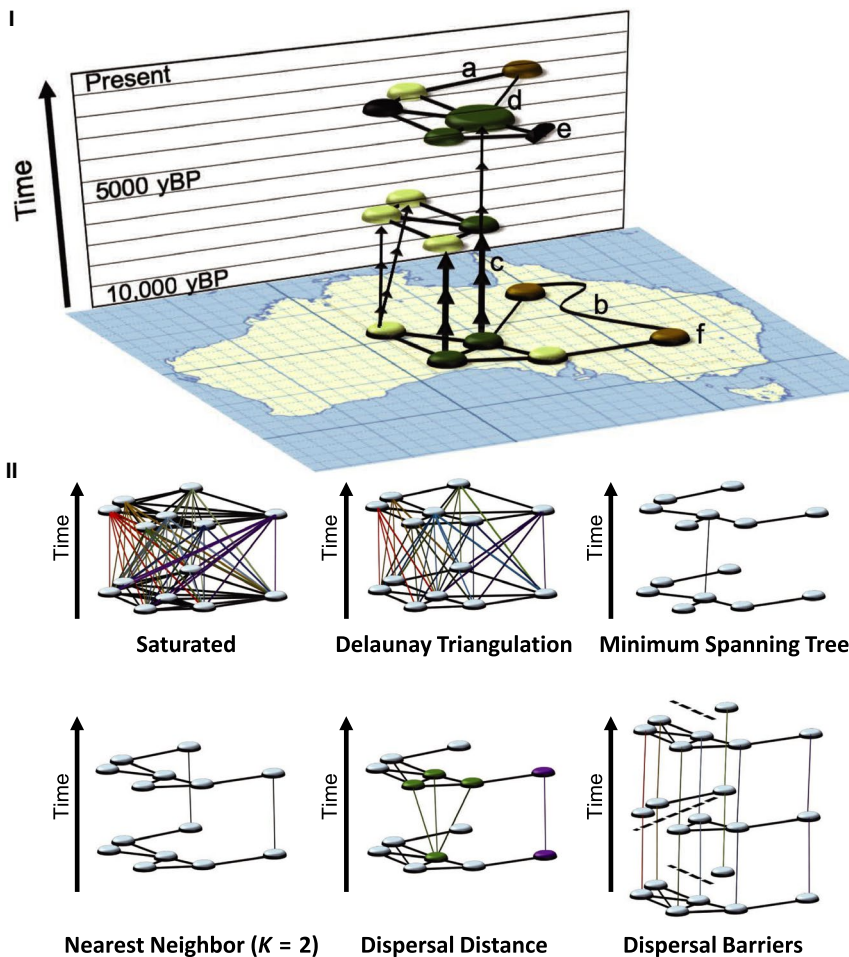
(I) Network models consist of nodes (dated and georeferenced individuals or populations) that may be connected by edges. Edge connections minimally represent which nodes can interact with one another but may also be associated with additional information. For instance, spatial attributes (horizontal connections) can include the simple Euclidean distance among samples (a) or represent the effective geographical distance among samples by modelling edges with a more complex shape based on underlying landscape features between nodes (b). Temporal attributes (vertical connections) of edges describe the temporal distance among samples (c). Additionally, edges can be bidirectional (a), indicating equal gene flow between nodes, or unidirectional (c) to represent one-way migration or to incorporate time. Spatiotemporal genetic attributes of edges might include migration rates or a measure of genetic distance among samples (indicated by different path widths as in b and c).

Temporal edge connections might also be associated with a drift parameter or measure of demographic change. Gravity models additionally incorporate information about the nodes. These parameters may include the size (d) and shape (e) of the habitat as well as parameters that affect habitat quality (indicated by node colours as in d and f). (II) Several methods are available for defining the spatiotemporal network topology and for testing the likelihood of different migration scenarios. Topologies can be described geometrically, such as by using 3D Delaunay triangulation to incorporate time, or minimum spanning tree or nearest neighbour algorithms which might use a combined index of spatiotemporal distance to determine connections among nodes. Alternatively, topology definitions may incorporate more realistic biological parameters, such as by only connecting locations that are within the species dispersal distance and/or have maintained temporal population continuity based on previous spatiotemporal population structure analyses. Informed connections might also include known changes in species dispersal barriers, such as cyclical sea level rise, land bridge availability, and glacial advance and retreat. Figure inspired by figures 10.1 and 10.2 of Murphy et al. (2016) and modified to incorporate aspects of temporal, as well as spatial, connectivity.

Another technique to predict spatiotemporal changes in metapopulation dynamics is the ancestry distribution model (ADM), which can forecast population-specific responses to climate change scenarios (Jay, François, Durand, & Blum, 2015). The ADM assumes that individuals that share geographical proximity as well as similar environmental conditions are also more likely to share genetic ancestry. Where there is a genuine relationship between an environmental factor and population structure (such as due to

local adaptations), climate changes in that environmental factor may therefore result in different population-specific responses within a species. By testing the correlation between admixture coefficients estimated with both genetic and environmental data versus admixture coefficients estimated with environmental data alone, important environmental variables associated with population structure can be identified. Those environmental covariates can then be adjusted in accordance with future climate change

models to predict how the populations are likely to respond to various climate change scenarios.

ADMs were used to predict how alpine plant species in the European Alps were likely to respond to increasing temperatures (Jay et al., 2012). Predicted responses to climate warming for most species included range expansion and contraction for warm-adapted and cold-adapted populations, respectively, and a spatial shift in the contact zone between the warm-adapted and cold-adapted populations. Significant population replacements might also be expected for some species under the most extreme climate change scenarios.

Although ADMs currently lack the capacity to incorporate heterochronous genetic data (Table 1), the models provide a good starting point for future methodological developments. In the meantime, ADMs may still be usefully applied in a historical context to answer several relevant research questions. For instance, using aDNA and palaeoclimate data, the analysis could be performed on relevant temporally grouped samples to evaluate whether predicted population responses to climate factors have remained consistent, or to assess if different environmental factors gained prominence in structuring populations through time. Alternatively, the use of historical samples would provide highly informative tests of the accuracy of the ancestry distribution models themselves. Revealing any potential biases of ADMs by testing how well they forecast current populations from historical populations and known climate change can only improve the method for future climate change predictions.

5.2 | Spatiotemporal population connectivity

It may also be of interest to test hypotheses of which environmental variables have most influenced gene flow among populations through time and investigate the spatiotemporal stability of these forces. To this end, population connectivity is also well-represented by graph theoretic approaches (Dyer & Nason, 2004; Garroway, Bowman, Carr, & Wilson, 2008), where the **nodes** represent individuals or populations and the **edges** represent connectivity or gene flow on the landscape. Time can be incorporated with the development of 3D networks, where temporal distances are represented in the vertical plane (Box 1). Genetic attributes of the nodes might include individual genotypes or population allele frequencies, while the edges may be attributed to genetic distance or migration rates (Murphy, Dyer, & Cushman, 2016). The genetic attributes represent observed connectivity and are used to assess the likelihood of hypothesized networks derived from environmental data. Several metrics can be derived from each graph topology to summarize the overall structural connectivity of the graph or to assess the relative importance of particular nodes in maintaining connectivity (Koen, Bowman, & Wilson, 2016; Murphy et al., 2016). The significance of a given topology can be assessed by comparison to simulated random distributions of graph topologies.

It is important to consider which edges are relevant to the system under study and determine whether and how to prune the edge set (Box 1; Dale & Fortin, 2010). In a spatiotemporal context, edges

describe the temporal and geographical distance between nodes, but do not need to be defined as the shortest straight-line distance between each node. Edges could represent other hypothesized space-time paths to test the likelihood of alternative migration corridors, or be used to test the temporal influence of environmental factors on connectivity by defining edges with least-cost paths (Adriaensen et al., 2003; Pinto & Keitt, 2009) or circuit paths (McRae, 2006) through dynamic landscapes. Edges may also be assigned a flow direction to model directional migration, such as for river networks or for spatio-temporal data, to ensure that connections among nodes only progress forward in time.

Although yet to be applied in an evolutionary context, graph theory has been employed to evaluate spatiotemporal connectivity in other applications, such as for identifying optimal transportation routes while taking into account time-fluctuating traffic density patterns (Fang, Shaw, Tu, Li, & Li, 2012), and to examine changes in recent temporal human migration patterns by comparing time slices of migration networks based on decadal census data (Davis, D'Odorico, Laio, & Ridolfi, 2013). Analogously, a graph theoretic approach might be used in an eco-evolutionary context in any number of ways, such as to compare multispecies connectivity histories to gain greater insight into the influences of past climatic factors (e.g., landcover change or glacial cycles) on population migrations; or to test hypotheses about the historical use of major migration corridors (Murphy et al., 2016).

Gravity models are an extension of the graph theoretic approach that can also be used to assess functional connectivity (Murphy, Dezzani, Pilliod, & Storfer, 2010). Gravity models describe gene flow as a linear function of three components: the distance among individuals or populations, the influence of the intervening landscape between habitat patches that affects dispersal success, and the production/attraction features of the habitat patches (Murphy et al., 2016). Thus, rather than just focusing on the effects of the intervening landscape **matrix** (i.e., between nodes or habitat patches), gravity models also consider features of the nodes themselves (i.e., habitat patches) that influence the probability of dispersing from the patch (e.g., production factors such as demography, carrying capacity, social behaviour), and the probability of staying in the same or a new habitat patch (e.g., attraction factors such as habitat quality that influence productivity and survival). The simultaneous consideration of both local (within node) and landscape (between node) features in a single analysis is a unique aspect of gravity models relative to other connectivity analyses, which focus solely on one aspect or the other. In a typical analysis, different combinations of variables with hypothesized influences on dispersal success and patch retention are evaluated in several candidate models to identify the model best representing the observed genetic data. As with any network model, the results are influenced by the selected network topology and edge pruning, and may be sensitive to missing nodes (Naujokaitis-Lewis, Rico, Lovell, Fortin, & Murphy, 2013).

Gravity models may be used with time series data, and several potential avenues for adapting this technique to heterochronous data have already been applied in other fields. For example, gravity

models can be used to identify parameters affecting contemporary species connectivity, the results of which could be extrapolated to other time periods, such as to generate hypotheses about the factors influencing past migrations, to predict connectivity under future climate change scenarios or to identify areas imminently susceptible to exotic species invasion (e.g., Bossenbroek, Kraft, & Nekola, 2001). Alternatively, the factors influencing connectivity can be compared in a time-slice manner to evaluate changes through time. For this approach, heterochronous samples are grouped according to time periods relevant to the study question and separate gravity models are generated for each time period and compared. This time-slice gravity model approach was used to identify factors that affect the spread of measles, as well as to infer whether those factors themselves changed through time (such as before and after vaccine availability, or depending on whether primary school was in session or not; Jandarov, Haran, Bjørnstad, & Grenfell, 2014). Finally, dynamic spatiotemporal networks can be constructed to directly incorporate a temporal component in the gravity models, so temporal changes in edge effects or node productivity/attraction can be evaluated. Although various analytical methods exist for evaluating change in spatiotemporal networks (e.g., Kim, Lee, Xue, & Niu, 2018), one approach is to use counts of production and attraction flows (i.e., dyad-specific directional migration estimates between nodes) aggregated across pre-specified temporal windows for each node pair to reveal spatiotemporal network connectivity patterns, and dynamic random effects models can be used to test the importance of bioclimatic features in predicting functional connectivity through time. Dynamic spatiotemporal gravity models have been used to analyse connectivity in space and time for various applications (e.g., for assessing global trade networks, Ward, Ahlquist, & Rozenas, 2013; or internet traffic patterns, Chen et al., 2015). These network models could certainly be adapted to a spatiotemporal landscape genetic framework to inform connectivity research questions, such as for identifying critical factors affecting species connectivity through time and evaluating how climate change has (or will) influenced population connectivity.

6 | IDENTIFYING DRIVERS OF SELECTION AND ADAPTATION ON THE LANDSCAPE

The hallmark of landscape genomics is the ability to evaluate functional and adaptive genetic variation on the landscape in relation to bioclimatic variables (Bragg, Supple, Andrew, & Borevitz, 2015; Manel et al., 2010; Schoville et al., 2012). Historical DNA samples are uniquely suited for this task as they provide a genetic record of adaptation, although this important application has yet to be fully realized. Numerous population genomics methods have been developed to take advantage of time series genetic data to detect loci that have undergone selective sweeps by quantifying the changes in allele frequency through time (e.g., Schraiber, Evans, & Slatkin, 2016; other approaches reviewed by Malaspinas, 2016). Related techniques can further be used to determine the strength of selection (e.g., Wilde

et al., 2014), estimate the selected allele age when adaptations arose in a population (Malaspinas, Malaspinas, Evans, & Slatkin, 2012), and evaluate if selection has been constant through time (e.g., Ludwig et al., 2015). While several of these aforementioned approaches account for population structure (e.g., Caye et al., 2016) and some even estimate spatially varying selection (e.g., Mathieson & McVean, 2013), these temporally explicit approaches do not incorporate spatial and bioclimatic information and, as such, are unable to infer the environmental drivers of natural selection. Not only does the association of climate variables with selected loci lend insight into the bioclimatic forces that have shaped contemporary genetic diversity, but these types of ecological association analyses have further been shown to have greater statistical power to detect selected loci than population differentiation genome scans, especially under weak selection (Mita et al., 2013; Villemereuil, Frichot, Bazin, François, & Gaggiotti, 2014). Still, most studies of evolutionary adaptation using ancient genetic samples have thus far been limited to attempts to ascertain spatiotemporal variation in phenotypes (e.g., Ollivier et al., 2013), describing genomic regions that have been lost or become fixed through time in various lineages (e.g., Meyer et al., 2012), or even to ascribing a temporal shift in allele frequencies to a shift in climate or habitat type—without actually testing whether the two data sets are correlated (e.g., Sandoval-Castellanos, Wutke, Gonzalez-Salazar, & Ludwig, 2017). To help realize the full potential of heterochronous samples for revealing spatiotemporal selection processes, here we review several techniques currently available for explicitly inferring the influence of environmental variables on adaptation that have potential for utilizing temporal data, and where available, describe the few example studies conducted to date that apply these approaches to samples from disparate time periods.

Regression methods are one of the most frequently used approaches for testing the correlations among environmental variables and allele frequencies at thousands of loci. Key differences lie in their technical implementation, such as whether the analyses are performed at the population-level or individual-level, and certain approaches are better suited for categorical environmental variables, for example.

6.1 | Logistic regressions

One of the first spatially explicit genomic methods developed was the spatial analysis method (MᴀᴛSAM; Joost, Kalbermatten, & Bonin, 2008) program, which not only identifies candidate genomic regions that have been influenced by selection, but also determines which environmental variables may be associated with the adaptive genomic change (Joost et al., 2007). MᴀᴛSAM (and other exploratory genome scan methods) is based on the premise that loci subject to selective forces will have atypical variation relative to the background genome, the latter of which is influenced more by whole genome processes of gene flow and genetic drift (Storz, 2005). MᴀᴛSAM relies on logistic regression to correlate the presence/absence of alleles at each locus with environmental data. The

statistical significance of the association between putative selected loci and the tested environmental variable is determined with likelihood ratio and Wald tests. MᴀᴛSAM, along with most of the other approaches described below, is a multiple univariate approach (i.e., separate, nonindependent tests are performed for each locus/environmental variable combination), for which a correction for multiple testing needs to be implemented (reviewed by François et al., 2016; Goeman & Solari, 2014).

Like most currently available genome scan methods, MᴀᴛSAM is not explicitly designed for heterochronous samples. However, the analysis is individual-based and so could easily accommodate heterochronous samples, as every individual's genotypic data would be associated with the environmental data from the relevant time-period when the individual lived. Thus, for scenarios or traits where constant selection through time can safely be assumed, the inclusion of heterochronous samples will probably increase the power of the tests, because allele frequency associations with climate data can be observed across both space and time. On the other hand, separate time-slice analyses (e.g., before, during and after a strong selection event) may be necessary where fluctuating selection pressure is suspected, as grouping all individuals together may mask important environment–genotype associations. MᴀᴛSAM was applied to identify genotype–environment associations through time in the zooplankton *Daphnia pulicaria* (Frisch et al., 2017). Two lakes were compared, one that has remained relatively stable since European settlement, and the other which has experienced higher eutrophication over the past century due to increased anthropogenic activity surrounding the lake. Dated lake sediment cores were used to obtain a temporal transect of *Daphnia* genotypes and nutrient accumulation rates. In the more polluted lake, significant microsatellite allelic associations with environmental proxies for lake eutrophication were identified.

Related approaches, such as generalized estimating equations, extend the logistic regression method by including a correlation matrix to account for biases resulting from population structure (Poncet et al., 2010). Also, the updated version of MᴀᴛSAM (SAMβADA; Stucki et al., 2017), in addition to being able to deal with population structure, also incorporates Moran's *I* to account for spatial autocorrelation effects. Of note, few of the current methods can explicitly account for temporal autocorrelation among allele frequencies and environmental predictors, which may increase false discovery rates.

6.2 | Linear regressions

SPATPG was specifically designed for the analysis of temporal data sets (Gompert, 2016). This program relates time-series genetic data to environmental variables of interest and can additionally accommodate fluctuating selection pressures through time. SPATPG functions similarly to the aforementioned genotype–environment correlation methods, although it exploits changes in allele frequencies with associated changes in the environment to derive putative selective pressures and selected loci. Like most other genotype–environment correlation methods, SPATPG assumes the environment has a linear effect on fitness. Thus, SPATPG performs well when selection is strong and the environment linearly influences single loci. However, accuracy declines with weaker selection, when selection pressures are nonlinear, or when selection is acting on polygenic systems.

SPATPG requires serial sampling of populations, so this approach is best suited for population monitoring applications. Also, even under strong selection, the power to detect selected loci declines significantly with decreasing samples size (e.g., power was reduced to only 40% even with as many as 25 samples/generation/population). Nevertheless, methodologies like these that begin to explicitly relate time series genetic and environmental data are essential for forming the foundation of a truly spatiotemporal analysis framework for studying adaptation.

6.3 | Linear mixed models

Linear mixed models control for heterogeneity in data sets due to nonindependence of the data, such as exists in pairwise genetic or environmental distances, or when there is a hierarchical structure to the data (i.e., where data in the lower level are likely to be correlated in some way, as for individual genotypes within a population; Bolker et al., 2009; Van Strien, Keller, & Holderegger, 2012). Linear mixed models tease apart the variance in the data set related to the tested predictor variables (fixed effects) and the variance in the data caused by nonindependence (random effects). As such, they are an important technique for reducing false positives stemming from pairwise distances and population structure in genome scan tests of genotype–environment correlations.

BAYENV is a Bayesian analysis program for testing the correlation between allele frequencies and environmental variables while accounting for population structure and uneven sample sizes (Coop, Witonsky, Rienzo, & Pritchard, 2010; Günther & Coop, 2013). This approach requires a subset of neutral control loci to build a null model that determines the covariance of alleles across populations, to account for the nonindependence due to population structure. Bayes factors are then calculated for each locus to determine the significance (relative to the null model) of genotype–environment correlations. BAYENV assumes the markers are in linkage equilibrium, although departures from this assumption are expected to affect primarily just the significance tests rather than the parameter estimates. BAYENV is most effective at detecting loci that have responded consistently to environmental variation across populations; separate regional and/or time slice analyses may be needed to tease out loci affected differently by local adaptation.

In one temporal application of BAYENV, time was incorporated directly as a driving variable to characterize directional selection over the past century of modern maize crop breeding (van Heerwaarden,

Hufford, & Ross-Ibarra, 2012), and this strategy may be useful for other temporal genetic studies, such as examining selection during species domestication. The BAYENV model may be less suitable for some historical DNA applications however, as it is meant to be population-based (i.e., applied to groups of related individuals that share a similar environment), although Coop et al. (2010) suggest that it could be applied at an individual level using individual allele frequencies (i.e., at a typical single nucleotide polymorphism [SNP] locus, heterozygotes have an allele frequency of 50%, while homozygotes have allele frequencies of 0% or 100% for the reference allele). Still, BAYENV can also accommodate evolving landscapes because the input file for environmental variables is population-specific; therefore, temporally relevant values could be used. Alternatively, depending on the temporal scale of the study, it may be of interest to examine only mean genotype–environment correlations to assess strong and consistent selection patterns across populations. This strategy was employed to investigate the spatiotemporal dynamics of Atlantic cod (*Gadus morhua*) and gain insight into local adaptation and recent selection processes for this species that may inform future climate change scenarios (Therkildsen et al., 2013). Separate null models were first estimated for historical populations and modern populations, and the mean of the two covariance matrices was used to create the null model for the final analysis. To generate data representing long-term environmental trends for each population, annual values for each environmental variable were averaged across the time span of the study (1948–2011). They found evidence of divergent selection and local adaptation related to seascape variables, suggesting the population genetic clusters may respond differently to future climate change.

GINLAND (Guillot, Vitalis, Rouzic, & Gautier, 2014) implements a spatially explicit generalized linear mixed model to test for significant genotype–environment associations. This technique evaluates the correlation between allele frequencies and environmental variables using linear or logistic regression and is suitable for the analysis of both categorical and continuous environmental variables. As the approach is spatially explicit, spatial autocorrelation is accounted for with a geographical distance matrix and the effects of neutral population structure are incorporated as a random factor. Like the other regression techniques, GINLAND can incorporate temporally relevant environmental values, permitting tests of genotype–environmental correlation through time.

Latent factor mixed models (LFMMs) are an extension of PCA that incorporate fixed effects to model environmental variables. These models use latent factors to account for unexplained genetic variation, which may arise from population structure or environmental variables that were not considered in the model (Frichot, Schoville, Bouchard, & François, 2013). The number of latent factors is generally based on the presumed number of populations, *K*, in the data set; when *K* = the total number of loci (and environmental variables are not considered), the method essentially performs a PCA. Underestimates of *K* increase the likelihood of false positive results, while overestimation of *K* reduces the power of the model. However, a key benefit of this method is the ability to simultaneously estimate the neutral population structure and the environmental effects on allele frequencies without having to define the structure (or determine putatively neutral loci) in advance.

6.4 | Ordination-based regressions

Several ordination methods are also appropriate for associating climate and allele frequency data to infer selection processes through time. Ordination methods often have faster computation times and are multivariate, permitting the analysis of multiple environmental variables on multiple loci at the same time. This may provide an advantage over univariate methods, because selection is often a polygenic process driven by multiple environmental variables (Forester, Jones, Joost, Landguth, & Lasky, 2016).

Three multivariate constrained ordination methods have commonly been used (with modern data) for assessing the influence of environmental factors on selection: redundancy analysis (RDA; Rao, 1964; Van Den Wollenberg, 1977), distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999) and canonical correspondence analysis (CCA; Ter Braak, 1986). Constrained ordination refers to the fact that these analyses perform a regular unconstrained ordination like PCA on the multivariate dependent variables (i.e., allele frequencies), but with the constraint that it is a function of the independent variables (i.e., environmental data), such as by regressing the genetic and environmental data and performing the ordination on the residuals.

In the context of genotype–environment associations, CCA, RDA and dbRDA all model the multivariate genotypic data as linear functions of the proposed multivariate environmental predictors (approaches to model nonlinear relationships have also been developed; e.g., Makarenkov & Legendre, 2002; Millar, Anderson, & Zunun, 2005). RDA is a constrained version of PCA and is thus appropriate for allele frequency data (Jombart, Pontier, & Dufour, 2009). dbRDA is analogous to RDA, except the genetic data are first ordinated with PCoA and the resulting univariate eigenvectors are then used as the response variables in the RDA, which can be regressed against the environmental variables with simple multivariate regression. CCA is the constrained version of correspondence analysis and is suitable for allele count data. These ordination analysis methods could be used to identify directional selection and pinpoint significant genotype–environment associations that have persisted over time by incorporating temporal environmental variation and associated historical genotypes. Additionally, all three analysis types can also be extended to partial out the effects of a third matrix, such as to account for neutral genetic structure, isolation-by-distance (IBD) or temporal autocorrelation (e.g., Frisch et al., 2017, see below).

These ordination approaches require that the explanatory environmental variables are uncorrelated, and the number of loci examined should be at least three times as large as the number of putative explanatory variables (Jombart et al., 2009). Identification of significant loci under selection may be performed by detecting outliers in the ordination space, such as loci that are 3*SD* from the mean axis

score (e.g., Forester et al., 2016). Selected loci can then be tested for their association with proposed environmental drivers using simple correlations with allele frequencies, or permutations (e.g., Pavlova et al., 2013).

Forester et al. (2016), Forester, Lasky, Wagner, and Urban (2017) compared the performance of several genotype–environment association methods (including BAYENV2, LFMM, RDA and dbRDA), at identifying loci under selection under a range of landscape heterogeneity scenarios, demographic histories, sampling schemes, gene flow rates and selection strengths. RDA and dbRDA were found to have lower false positive rates than LFMM, but under weak selection there was a trade-off between power and false discovery. Although LFMM accounts for population structure with the user-defined number of latent factors, selecting an appropriate K is difficult when populations are clinal, rather than discrete. In these scenarios, the constrained ordination methods are better able to correct for patterns of IBD when dispersal is low and thus avoid spurious genotype–environment correlations. Additionally, the constrained ordination approaches were found to be more robust to sampling scheme relative to the univariate approaches tested, which could benefit studies incorporating historical specimens that may be limited to opportunistic sampling.

While it is important to account for population structure in any analysis of selection, it may also be of interest to identify climate factors associated with population structure itself, as this could indicate local adaptations. Constrained ordination methods like CCA, RDA and dbRDA are conducive to these analyses as well (François & Waits, 2016). In this case, rather than seeking only functional loci that are associated with environmental variation, local adaptation would be indicated by significant correlations between environmental variables and both adaptive and neutral loci. For instance, CCA was used to determine if the contemporary population structure of mule deer (*Odocoileus hemionus*) was due to local adaptation to separate ecological niches, or to long-standing isolation from LGM refugia (Pease, Freedman, & Pollinger, 2009). Similarly, dbRDA was used to assess whether environmental variables associated with lake eutrophication explained genetic differentiation among *Daphnia* populations through time, while partialling out the effects of temporal autocorrelation (Frisch et al., 2017).

6.5 | F_{ST}-based genome scan with environment

BAYESCENV is a genome scan approach for specifically evaluating local adaptation by comparing the likelihood of three different models: a neutral model, a locus-specific model of differentiation that is unrelated to the environmental variable being tested, and a local adaptation model for a given environmental variable (Villemereuil & Gaggiotti, 2015). Like BAYENV, this is a population-based test, requiring allele counts at each locus per population. However, unlike the methods described above which test for correlations between genotypes and the environment, BAYESCENV identifies outlier loci that exhibit atypical F_{ST} values among populations. BAYESCENV then

evaluates local adaptation to environmental variables by testing the relationship between locus-specific genetic and environmental differentiation among populations, relative to the neutral and alternative models.

Although we were unable to find any example applications of this approach to studying spatiotemporal adaptation, it may be suitable for several reasons. First, F_{ST} is a useful genetic distance for spatiotemporal analyses because it is related to coalescence time (Slatkin, 1991) and increases predictably with increasing temporal (as well as spatial) distance among populations (Duforet-Frebourg & Slatkin, 2016; Skoglund, Sjödin, Skoglund, Lascoux, & Jakobsson, 2014). Also, environmental parameters are expected to be coded in terms of distance to a reference quantity (e.g., altitude relative to sea level), which may be particularly useful for temporal analyses, as environment values could be parameterized as the relative change at a site since some time in the past or even relative to present-day values.

6.6 | Nonlinear associations

Generalized dissimilarity models (GDMs; Ferrier, Manion, Elith, & Richardson, 2007) and gradient forests (GFs; Ellis, Smith, & Pitcher, 2012) are two unique models proposed by Fitzpatrick and Keller (2015) for identifying significant genotype–environment correlations. These approaches model nonlinear functions of genotype–environment associations. GDMs are similar to partial Mantel tests in that they are both regressions of dissimilarity matrices, in this case of genetic distance, geographical distance and environmental variables. However, rather than a linear regression, a GDM calculates a monotonic I-spline turnover function and the percentage deviance explained by the predictor variable is used to determine model fit (Box 2). By explicitly accounting for geographical distance, the technique reduces bias stemming from spatial autocorrelation.

GFs are built on species-level random forest analyses (here, using individual loci instead of species) to extend the approach to community-level (i.e., genome-level) applications. GFs use machine-learning to iteratively split the genomic data along an environmental gradient to determine how well the environmental factor explains the variance in the allele frequencies. The split importance (i.e., the relative amount of genomic variation explained when the allele frequencies are divided at the environmental split value being tested) is cumulatively summed for each point along the environmental gradient. The algorithm builds a nonlinear turnover function in a staircase-like fashion to identify loci suggestively correlated with environmental gradients (Box 2). Thus, loci that lack an association with a given environmental gradient will fail to accumulate much "split importance," because little of the frequency variation will be explained at any environmental value, resulting in a relatively flat function. In contrast, loci that are significantly influenced by the tested climate variable will rapidly gain explanatory power along the environmental gradient, resulting in a function that describes a high relative importance of the environmental variable for explaining allele frequencies at that locus. The locus-specific functions are then aggregated across all loci

## BOX 2 Assessing genotype-environment correlations through time

General Research Questions:
What loci have been influenced by selection over time? When and where? What were the driving environmental factors?

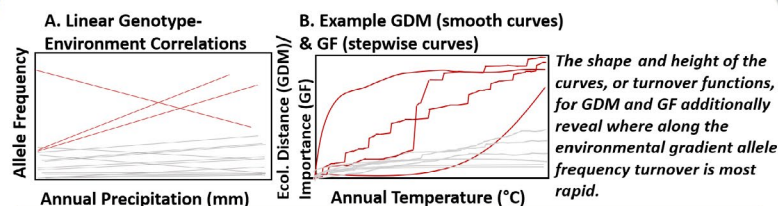### I. Collect dated and spatially-referenced genetic data

Population-level   Individual-level
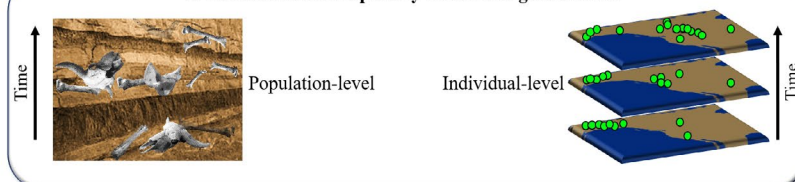
II. Obtain relevant environmental data from same locations and times

Categorical   Continuous
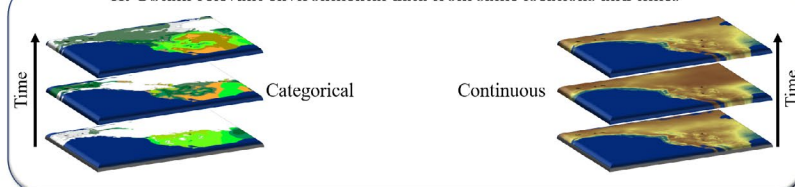
III. Determine correlations between genotypes and environment

		Individual- & Population-level Sampling	Population-level Sampling Only
Suitable for both Categorical & Continuous Environmental Variables	**Linear, Univariate**	SAM/SAMBADA GEE	
Continuous Environmental Variables Only		GINLAND	BAYENV SPATPG BAYESCENV
	Nonlinear, Univariate	GDM GF	
	Linear, Multivariate	LFMM RDA DBRDA CCA	

IV. Conduct significance testing and interpret results

A. Linear Genotype-Environment Correlations

Allele Frequency

Annual Precipitation (mm)

B. Example GDM (smooth curves) & GF (stepwise curves)

Ecol. Distance (GDM)/ Importance (GF)

Annual Temperature (°C)

The shape and height of the curves, or turnover functions, for GDM and GF additionally reveal where along the environmental gradient allele frequency turnover is most rapid.
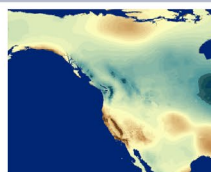
Although analysis output is usually tabular, the graphs (A, B) present a visual depiction of genotype-environment correlations, where certain loci may be identified as having a significant association with a particular environmental variable (red lines).
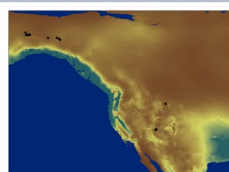
C. LGM Precipitation   **D. Mid-Holocene Precipitation**   **E. Change in precipitation LGM to mid-Holocene**
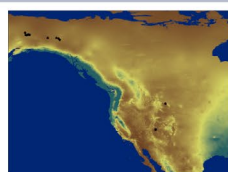
I. Sampling is conducted at either the population level (e.g., annual breeding site surveys; multiple individuals per layer in a palaeontological site temporal transect) or individual level (e.g., opportunistic museum sample collections, long-term systematic field studies) for samples with known locations and dates. II. Environmental data relevant to the organism under study and the research question are also obtained for the same locations and time periods. Environmental data may be categorical (e.g., land cover types) or continuous (e.g., mean annual precipitation). III. Several analysis approaches (discussed in the text) are available for conducting genome scans for selection and assessing the strength of association with predictor environmental variables through time. These analyses can identify loci with alleles or allele frequencies that are significantly correlated with environmental gradients and thus suggest which environmental factors have had (and may continue to have) strong influences on species through time. IV. Certain analyses may be more effective than others for a given data set, depending on whether selection resulted in selective sweeps at a few loci or polygenic adaptation, and whether the genotype–environment relationship is linear (A) or curvilinear (B). Additionally,

BOX 2 (Continued)

mapping genotype–environment correlations on the landscape may provide further insights when the results are projected to other time periods. For example, for environmental variables discovered to be significantly associated with genotypes (and presumably fitness), mapping known or predicted climate change between time periods (C, D) can highlight areas experiencing the most drastic changes (E) and, by extension, where populations have been (or will be) most stressed to keep pace with climate change. Alternatively, the allele frequency turnover functions created by GDM and GF analyses can reveal where small changes in an environmental variable may necessitate large changes in allele frequencies. For studies covering a vast temporal extent, analyses performed on all individuals can reveal consistent environmental pressures and genetic responses (that may have been replicated in space and time). Alternatively, time slice analyses may expose varying environmental selection regimes through time. There is still rich opportunity here for the development of analyses that can dynamically evaluate genotype–environment correlations through time and quantify the consistency of selection pressure of different environmental variables in space and time. Data depicted in (c) and (d) are from Hijmans, Cameron, Parra, Jones, and Jarvis (2005).

to create a genome-level function. GFs can accommodate correlated or interacting predictor variables, although it does not account for spatial autocorrelation.

For both GDMs and GFs, the height and shape of their turnover functions describe the relative importance of environmental predictors in influencing genetic change and how the rate of change varies along the environmental gradient. Thus, these methods are suitable for identifying both gradual clinal allele frequency changes along environmental gradients, as well as sharper threshold boundaries that define local population physiological tolerances.

GDM and GF approaches were applied to explore adaptive variation in the balsam poplar (*Populus balsamifera*) and to predict the species vulnerability to future climate change (Fitzpatrick & Keller, 2015). By visualizing the turnover functions on the landscape, balsam poplar populations with significantly different allele frequencies associated with climatic variables could be identified. Future climate change models were further used to predict population-level vulnerability of balsam poplar to climate perturbations by identifying geographical regions where small changes in temperature would predict abrupt changes in allele frequencies. In a related example, Rosauer et al. (2014) used a GDM approach to evaluate phylogenetic turnover relative to environmental predictors among Australian frog species. Using only modern data, the deepest phylogenetic branches were found to have reduced model fit with contemporary environmental variables, as species–environment relationships had changed through time.

By incorporating historical genetic samples and relevant palaeoenvironmental data, GDM and GF approaches could improve inferences of environmentally driven phylogenetic relationships and adaptation. For instance, time could be incorporated explicitly as a variable, to potentially determine the timings of selective sweeps (GF) or to evaluate selection while controlling for temporal autocorrelation (GDM). Moreover, identifying significant genotype–environment correlations of multiple spatiotemporal populations not only can help to illuminate variable selective pressures in space and time, but mapping these turnover functions on the landscape and projecting forward to known climate changes can further identify where (in space and time) species' populations were most stressed.

Relating this information to species' population history would have immense implications for conservation biology, by furthering our understanding of the conditions in which populations are able to respond to climate change through migration or adaption versus population replacement or extinction.

Methods such as these, which explicitly test genotype–environment correlations, have thus far only rarely been applied to temporal studies of adaptation (Table 1). With the incorporation of spatiotemporal data, however, these techniques may be even more powerful at detecting selected loci and elucidating the selective environmental forces. Furthermore, by identifying associations between allele frequencies and environmental variables that vary not only in space but also in time, genotype–environment association methods can effectively detect drivers of adaptation and selective sweeps as they occurred in temporal populations. In this manner, by fully exploiting the information contained in time-series genetic samples that span key climatic and landscape changes, we will have the ability to transform our knowledge of the factors that have shaped contemporary biodiversity and to greatly broaden our insight into extinction processes.

7 | CONCLUSION

With the explicit integration of spatiotemporal genetic and environmental data, spatiotemporal landscape genetic techniques promise to revolutionize our understanding of evolution and the role of climate and landscape change on population processes. The potential applications are vast, from understanding bioclimatic influences on range shifts and population dynamics, to fully recognizing the environmental factors that have driven adaptation through time. Robust insight into a number of controversial evolutionary questions could be gained with a spatiotemporal landscape genetics approach, such as the respective roles of climate and humans in megafaunal extinction (e.g., Cooper et al., 2015; Metcalf et al., 2016; Prescott, Williams, Balmford, Green, & Manica, 2012; Sandom, Faurby, Sandel, & Svenning, 2014), or the origin of species domestication (e.g., Frantz et al., 2016; Pang et al., 2009; Thalmann et al., 2013; Wang, Peng, Yang, Savolainen, & Zhang, 2016). No

longer restricted to inferring simply *how* populations have changed through time, spatiotemporal landscape genetic analyses open the door to understanding *why*.

In addition to informing evolutionary history, spatiotemporal landscape genetics can lead to a greater realization of the potential for aDNA to inform today's conservation crisis (Dietl & Flessa, 2011; Leonard, 2008). By assessing actual responses to past climate change, we may be able to predict species responses to future climate change with much greater accuracy. With the direct integration of genomic and bioclimatic data over time, we can clarify the factors that influence when species are likely to respond to climate perturbations with phenotypic plasticity, by adapting in situ, migrating or going extinct. Conservation biology theory can be directly tested with the integration of palaeogenetic and palaeoclimate data, such as by revealing the predicted limits to adaptation for range edge populations (Hampe & Petit, 2005). Improved spatiotemporal models for analysing genetic and environmental data can even be used to genetically monitor adaptation and species-specific responses to climate change (Hansen et al., 2012), or inform invasive species management by revealing bioclimatic factors influencing range shifts and predicting the likelihood of establishment and spread of invasive species (Waters & Grosser, 2016). Modelling dynamic changes in landscapes and population genetics will also be critically important for conservation biology research and applications such as disentangling the historical influence of climate drivers from anthropogenic factors such as exploitation.

Presently available methods vary in their ability to incorporate temporal data and there is ample opportunity for novel research and future methodological advancements. Three strategic areas of research and innovation will be instrumental for the strengths of spatiotemporal landscape genetics methods to be fully realized. First, greater application of the currently available methods to historical data sets can complement and refine our current understanding of evolutionary processes for a wide variety of organisms. Employing these techniques in a variety of study systems and simulation scenarios will further highlight analytical strengths and weaknesses and identify areas for methodological development.

Second, increased effort is needed to develop spatiotemporal population genetic theory, particularly regarding how population allele frequencies behave in space and time and under a range of evolutionary scenarios. For instance, Duforet-Frebourg and Slatkin (2016) developed a mathematical theory that extends the stepping stone model of IBD to a model of isolation-by-distance-and-time. Additionally, most landscape genetics metrics assume drift-migration equilibrium and ignore mutation, which are fallacious assumptions for studies with large temporal **extents**. Heterochronous sampling has been shown to inflate many classical measures of genetic diversity and affect signals of population genetic structure, probably due to the unaddressed role of drift and mutation processes (Depaulis, Orlando, & Hänni, 2009). Thus, the incorporation of genetic drift and mutation dynamics in spatiotemporal landscape genetics metrics will be an important and necessary advance. Theoretical developments

such as these are bound to strengthen the design of future spatiotemporal landscape genetic analytical methods and interpretations of spatiotemporal data. Moreover, a strong theoretical basis will determine the validity of analyses for a given data set and inform appropriate aDNA sampling schemes.

Finally, additional research and development is needed to better adapt current methods or to design new analysis techniques that can explicitly incorporate spatiotemporal population genetic theory and simultaneously analyse both time-series genetic and landscape data. This will provide the tools needed to more effectively investigate bioclimatic drivers of evolution across a broad range of species and life history strategies. Future models may even be able to incorporate more complex biotic interactions to thus attain an even more complete picture of evolutionary history, such as by including competition or predator–prey interactions as species enter new habitats, identifying co-evolutionary patterns among species, revealing climate change influences on biodiversity and community ecology through time (Bálint et al., 2018; Thomsen & Willerslev, 2015), or understanding abiotic impacts on hybridization and introgression (Hand, Lowe, Kovach, Muhlfeld, & Luikart, 2015). Recognizing ancient epigenetic changes and the role of phenotypic plasticity will additionally be critical to further our understanding of species evolution (Gokhman, Meshorer, & Carmel, 2016; Llamas et al., 2012; Orlando & Willerslev, 2014). However, the relative importance of epigenetic modifications for rapid adaptation to climate change will not be fully appreciated without spatially explicit analyses and direct links to temporally fluctuating environmental variables.

We have highlighted the myriad possibilities for how spatiotemporal bioclimatic data and integrated analyses can inform palaeogenetic and molecular ecology research. Undoubtedly, a much deeper mechanistic understanding of environmental impacts on population processes can be gained with the assimilation of time-series environmental changes and genomic responses. With greater incorporation of heterochronous genetic and environmental data we will achieve considerably richer insights in ecology and evolution—which only a spatiotemporal landscape genetics perspective can provide.

AUTHOR CONTRIBUTIONS

L.E.F. conceived, researched and wrote the manuscript. A.I.K. and B.L. critiqued and edited the manuscript.

GLOSSARY

Autocorrelation: When a variable is correlated with itself, typically spatially or temporally. In spatiotemporal landscape genetics, autocorrelation represents the tendency for individuals to be more similar genetically simply due to their spatial or temporal affinity, resulting from restricted dispersal and heredity. Likewise, environmental variables tend to be more similar the closer the measurements are in space and time. Spurious associations may be detected when testing correlations among genetic and environmental data if autocorrelation is not considered.

Bioclimatic: Pertaining to the interaction between environmental factors and living organisms.

Edge: Links in a network-based analysis, typically the spatiotemporal distance between the individuals or populations under study and associated environmental data between sampling locations and time points. Edge-based spatiotemporal population genetic analyses involve comparing the genetic distance and spatiotemporal geographical distances between individuals or populations. The spatiotemporal geographical distance may additionally be weighted by the hypothesized influence of the intervening landscape through time.

Extent: The full spatial boundary of the study area and temporal boundary of the time frame under consideration.

Heterochronous: Refers to disparate time periods. Antonym of contemporaneous or isochronous.

Lag: The temporal interval between a change in relevant climate or landscape variables and a detectable genetic response in the population.

Matrix: In a landscape genetics context, a landscape is typically viewed as a composite of patches or "islands" of suitable habitat for the organism under study, embedded in the "sea" of the surrounding landscape matrix. The landscape matrix is thus composed of a range of less suitable abiotic factors and habitat types.

Node: Points in a network-based analysis, typically the individual or populations under study and associated environmental data at those sampling locations and time periods. Node-based spatiotemporal population genetic analyses typically involve comparing allele presence/absence or allele frequencies for each individual/population, with climate or landscape parameters associated with the individual/population location at that time.

Sampling interval: The spatial and temporal sampling frequency or distance among successive samples. For instance, a forest might be sampled annually (temporal sampling interval) along transects every 500 m (spatial sampling interval). Also known as lag in some fields, although we reserve this term for the definition noted above.

Space-time cube: A three-dimensional representation of the landscape where each voxel (3D pixel) represents a land cover or climate variable value at a given location and point in time. Longitude, latitude and time are represented by the x-, y- and z-axes, respectively.

Space-time path: The route depicting an object's movements across space and through time. In a spatiotemporal landscape genetics context, this would be a spatiotemporal trajectory linking descendant individuals or populations in space and time across a changing landscape as represented by a space-time cube.

Time slice: Data that may be considered contemporaneous within a certain time frame. Used throughout to refer to analyses that cannot incorporate heterochronous data directly, but multiple analyses may be run for different time periods and compared.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix

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