Title: Space-for-time substitutions in climate change ecology and evolution

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Abstract

In an epoch of rapid environmental change, understanding and predicting how biodiversity will respond to a changing climate is one of the most urgent challenges faced in ecology and evolution. Since we seldom have sufficient long-term biological data to use the past to anticipate the future, spatial climate-biotic associations are often used as a proxy for predicting biotic responses to climate change over time. These ‘space-for-time substitutions’ (SFTS) have become near ubiquitous in global change biology, but with different subfields having largely developed in isolation. We review how climate-focussed SFTS are used in four subfields of global change biology, each focussed on a different response type – population phenotypes, population genotypes, species’ distributions, and ecological communities. We identify the similarities and differences between the methods, the limitations and opportunities within each subfield, and highlight the potential for different subfields to gain insight from each other. While SFTS are used for a wide range of applications, two main approaches are applied across subfields: *in situ* gradient methods (including ecological niche modelling) and transplants (common gardens and reciprocal transplants). All SFTS methods and applications share a number of key limitations and assumptions relating to (i) the *causality* of identified spatial associations and (ii) the *transferability* of these relationships over time. Despite their widespread use, key assumptions in SFTS remain largely untested, including the fundamental assumption that climate-biotic relationships observed over space are causal and are equivalent to those occurring over time. We highlight how the robustness of SFTS can be improved by addressing these assumptions and limitations, with a particular emphasis on where approaches could be shared between subfields.

Key words: Space-for-time substitutions, climate change, ecology, evolution, reciprocal transplants, common gardens, *in situ* gradients, ecological niche models, biotic lags, biotic offsets

Contents

I. Introduction

Environmental conditions and the biotic responses (see VII. Glossary) that they elicit can vary over both space and time. For instance, aspects of climate that differ on multiple spatial and temporal scales, such as temperature and precipitation, drive ecological trends across all aspects of biodiversity. These trends range from population phenotypes (Bergmann, 1848; Darwin, 1859) and genotypes (Bradshaw & Holzapfel, 2001), to species’ distributions (Merriam, 1894; Grinnell, 1914) and biotic communities’ function and composition (Moritz *et al.*, 2008). As we progress through the Anthropocene – an epoch defined by rapid human-induced global change (Lewis & Maslin, 2015) – the biotic impacts of climate change are becoming increasingly apparent (Walther *et al.*, 2002; Root *et al.*, 2003; Scheffers *et al.*, 2016), as is the urgent need to understand and predict how biodiversity is responding and will respond to rapid contemporary climate change. Given that ecological processes operate over time, predicting the biotic impacts of future climate change would ideally use long-term monitoring data to directly observe temporal associations and project these into the future (time-for-time) (Roy *et al.*, 2001; Simmonds *et al.*, 2020). However, long-term ecological time-series data are rare (Estes *et al.*, 2018), in part because most research funding lasts less than 5 years (Lindenmayer, 2018). Along with the urgency of predicting biotic impacts of global change, this has motivated using alternative approaches that can generate predictions rapidly (Blüthgen *et al.*, 2022), often from existing data or relatively small datasets that can be generating during single grants. For these reasons, the last few decades have seen an increase in the use of spatial data to understand climate-biotic relationships (see VII. Glossary), with three main approaches used: (i) Space-time equivalence (see VII. Glossary) – where spatial and temporal data are considered together under the explicit or implicit assumption that climate-biotic relationships are the same in space and time (Shutt *et al.*, 2019; Yasuhara *et al.*, 2020); (ii) Space-time comparison (see VII. Glossary) – where climate-biotic relationships estimated separately in space and time are compared providing insights into the processes operating (Phillimore *et al.*, 2010) (Table 1aii); and (iii) Space-for-time substitution (SFTS; see VII. Glossary) – where spatial climate-biotic relationships are used as a substitute for temporal climate-biotic relationships to predict changes over time (assuming space-time equivalence) (Pickett, 1989), and which are the main focus of this review. Note that in space-time comparisons there is generally an implicit SFTS in that the spatial biotic response to climate is assumed to capture the equilibrium (see VII. Glossary) relationship.

Studies that employ SFTS to predict biotic responses to future climate change have been conducted across a variety of spatial climate gradients including elevation/altitudinal (Zografou *et al.*, 2020), latitudinal (De Frenne *et al.*, 2013) and urbanisation (heat islands; Lahr, Dunn & Frank, 2018; Diamond & Martin, 2021) gradients, each of which has different strengths and weaknesses (Verheyen, Tüzün & Stoks, 2019). One advantage of SFTS is the relatively straightforward logistics of data collection compared to time-series approaches. Moreover, where historic time-series are lacking, it may provide the most feasible and tractable approach for predicting the ecological and evolutionary impacts of climate change. While the advantages of using SFTS are many, the method has inherent limitations that need to be acknowledged, explored, and minimized for it to be make best use of research effort, as well as to increase understanding and predictions. Namely, for all biotic responses, SFTS relies on the fundamental, and often implicit, assumption that climate-biotic relationships observed in space are predictive of those that occur over time; an assumption that is rarely tested (Phillimore *et al.*, 2010; Isaac *et al.*, 2011).

The use of SFTS in global change research has progressed somewhat independently across the subfields focussing on different biotic responses. Therefore, this review aims to synthesise the use of SFTS across these biotic responses, identifying parallels between approaches and highlighting instances where approaches developed in one subfield may be applicable in others. We focus on four broad classes of biotic responses where SFTS are used: population phenotypes, population genotypes, species' distributions and ecological communities (Table 2). We first describe the general approaches applied across different biotic responses and highlight the limitations relevant to all subfields. Second, we consider each subfield in turn, focussing on the SFTS methods employed, their applications and the insights gained, and any subfield-specific limitations. Third, we discuss the broad challenge of validation that is pertinent to SFTS in all subfields. Finally, we identify opportunities for improving the reliability of SFTS and for cross-fertilisation of ideas between different subfields. While the focus of this review is on SFTS across climate gradients, many of the insights also apply to SFTS across other types of environmental gradients (e.g. land use intensity, exploitation pressure).

II. Commonalities of SFTS approaches

There are two main method types that are employed across all subfields to investigate biotic responses to environmental variation over space: *in situ* gradient approaches and transplant experiments (see VII. Glossary). These are compared in Figure 1 and Table 1. *In situ* gradient methods involve studying biotic states (see VII. Glossary) at multiple sites along a climate gradient, thereby allowing climate-biotic associations to be estimated (Fig. 1a, Table 1a; Dunne *et al.*, 2004). A variant of this approach that was developed for studying species distributions is the ecological niche model (ENMs; see VII. Glossary, Section III(3)), which are variously termed environmental niche, species distribution, (bio)climatic envelope and habitat suitability models (see Peterson & Soberón, 2012; Araújo & Peterson, 2012). An attraction of the *in situ* gradient method is the relatively low logistical hurdle to data collection, meaning that spatial replication (i.e. number of sampling locations) is often in the tens to thousands. However, the standard *in situ* correlative approach in isolation is usually uninformative about the processes that generate the spatial pattern of a biotic state, such as the relative contributions of short-term processes (e.g. phenotypic plasticity; see VII. Glossary) versus longer term equilibrium responses (Table 1a).

The second SFTS method uses transplant experiments, either to a common garden (see VII. Glossary) environment (Fig. 1b; Table 1bi) or as a reciprocal transplant (see VII. Glossary) between pairs of sites (Fig. 1c, Table 1bii). Transplant experiments can yield information on the processes (e.g., plasticity versus genetic divergence) that generate spatial climate-biotic associations (Turesson, 1922; Nooten & Hughes, 2017; Stamp & Hadfield, 2020). However, the logistics of transplant experiments often leads to low levels of spatial replication (Johnson *et al.*, 2021), which makes it difficult to identify the causal driver(s). There are also many taxa for which transplant experiments are challenging or unfeasible.

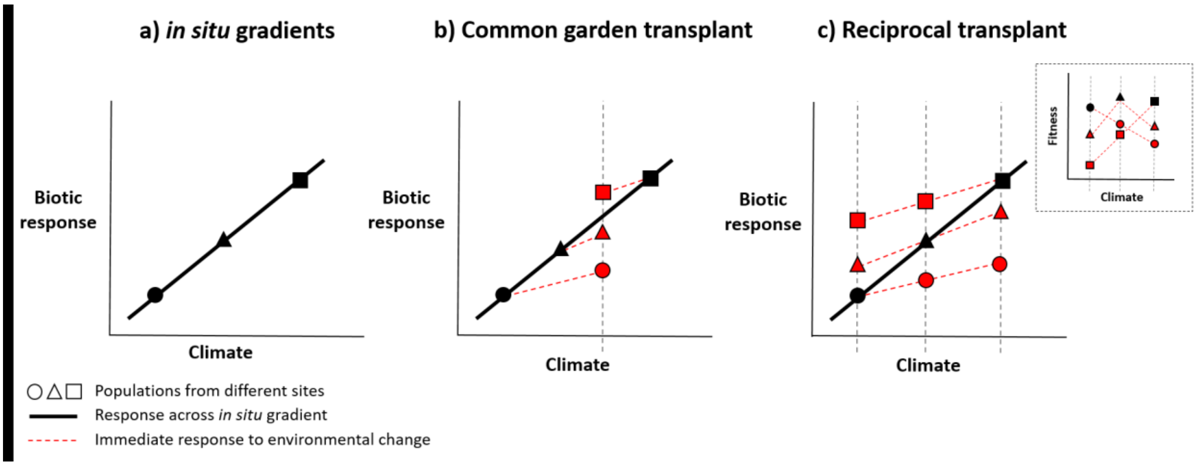

Figure 1: *Methods used to identify spatial climate-biotic associations for SFTS: (a) in situ gradients, (b) common garden transplants, and (c) reciprocal transplants. Across all plots, shapes represent populations that have different sites of origin. (a) in situ gradient approaches, where biotic states observed at sites across a climate gradient are used to model climate-biotic associations (black line). (b,c) transplant approaches where organisms are moved across space into different environments. Here, dashed red lines indicate an immediate response to a new environment (e.g. phenotypic plasticity). Transplant approaches are (b) common gardens, where organisms from different sites are moved into a shared environment and (c) reciprocal transplants, where organisms from different sites are reciprocally moved into each other's environments. The insert in (c) shows the unique case when the biotic state is fitness and each population has higher fitness at its site of origin (satisfying the local > foreign fitness criterion). Note that linear associations are depicted here but responses could be non-linear.*

Two extensions of the SFTS approach have been developed to predict the threat of climate to biodiversity. These involve identifying and quantifying either (i) a biotic offset (see VII. Glossary), the difference between the observed biotic state at site and the predicted equilibrium state at that site in a future climate (Fig. 2a) (Fitzpatrick & Keller, 2015; Frank *et al.*, 2017) or (ii) a biotic lag (see VII. Glossary), the difference between the observed biotic state at a site and the predicted equilibrium state at that site under the current climate (Fig. 2b). One extension of this involves quantifying a biotic lag in terms of spatial distance: a shift in a biotic state and a shift in climate in a given time period are each quantified in terms of the equivalent geographic shift (Balanyá *et al.*, 2006), and the difference represents the 'distance of biotic lag' (see VII. Glossary; Fig. 2c) (Devictor *et al.*, 2008, 2012; Ash, Givnish & Waller, 2017).

SFTS are widely used due to their utility for generating predictions in the face of an urgent need (Fukami & Wardle, 2005), but suffer from limitations that apply across subfields and, in the absence of validation, may undermine the reliability of predictions. Table 3 provides a non-exhaustive overview of key limitations of SFTS, which fall into two broad categories: (i) Causality: causal associations may not always be captured with the correlative methods used and (ii) Transferability: reliable projection relies on the assumption that spatial and temporal associations are equivalent and that associations will hold under future climates, including novel climates.

III. Application of SFTS to climate-biotic relationships

(1) Population phenotypes

Correlations between spatial climate gradients and phenotypes have long been observed, including well known relationships with body size (Bergmann, 1848), phenology (Hopkins, 1919), and seasonal coat colouration (Zimova *et al.*, 2020). Consequently, SFTS informed by *in situ* gradients and transplant experiments have been widely used to understand and predict the effects of climate change on a broad array of traits including morphology (Jaramillo *et al.*, 2017; Stelling-Wood, Poore & Gribben, 2021), phenology (Kramer, 1995; Ford *et al.*, 2016), life history (Etterson, 2004; McCabe, Aslan & Cobb, 2021), behaviour (Refsnider *et al.*, 2018), physiology (Pratt & Mooney, 2013; Logan, Cox & Calsbeek, 2014) and gene expression (Swaegers, Spanier & Stoks, 2020).

Where *in situ* gradients are used to generate a space-for-time prediction, the two extreme implicit assumptions are that: (i) the spatial response is entirely driven by phenotypic plasticity and so the phenotypic response is predicted to be rapid (Jaramillo *et al.*, 2017; Zografou *et al.*, 2020), or (ii) adaptation is responsible for the correlation, with the implication being that a change in climate will lead to directional selection on the trait and adaptation over multiple generations. Though very often, the predictions arising from such studies are vague, with no quantification or indication of timescale and thus, the assumed mechanism of response is ambiguous. Where phenotype and climate data are available in space and time, it is possible to make space-time comparisons, where climate-phenotype relationships are estimated in time as well as space. This information has been used to draw inferences about (i) the contributions that climate-mediated phenotypic plasticity and local adaptation (see VII. Glossary) make to the spatial relationship between spring temperature and phenotypes (Phillimore *et al.*, 2010; Hodgson *et al.*, 2011; Roy *et al.*, 2015; Delgado *et al.*, 2020) and (ii) biotic lags and offsets (Fig. 2) (Phillimore *et al.*, 2010, 2016). The space-time comparison approach can readily be applied to existing spatiotemporal phenotypic data, but is likely to be especially sensitive to third variables, such as gradients in photoperiod, precipitation or winter temperature (Tansey, Hadfield & Phillimore, 2017). Similarly, modelling phenotypes as a function of long-term and short-term climate values can also provide insights into the relative contributions of plasticity and genetic variation to spatial trait-climate relationships (Fréjaville *et al.*, 2019).

Transplant experiments offer the attraction of robust estimation of the contributions that phenotypic plasticity and genetic divergence (including local adaptation) make to spatial variation in phenotypes (Turesson, 1922) (Table 1b), and thus may make to temporal changes. Plasticity can be estimated as the difference in the mean population phenotype between the home and transplanted environment (Stamp & Hadfield, 2020). Quantifying plasticity with respect to a particular climate driver is more difficult, requiring either climate manipulation across multiple common garden environments or estimation of the correlation between climate differences and plasticity-mediated phenotypic divergence between sites. A strength of the common garden design is that it controls for plastic response to the home environment, such that any difference in the *phenotypes* of F2 generations in a common garden (i.e. once maternal effects have been controlled for) is usually attributed to genetic divergence, rather than plasticity (assuming that transgenerational plasticity is low). In comparison with the common garden design, a reciprocal transplant design affords the additional strength of facilitating fitness comparisons across home vs away and/or local vs foreign environments, such that one can infer whether populations are locally adapted (Kawecki & Ebert, 2004; Blanquart *et al.*, 2013). Where the focus is on whether a specific trait exhibits local adaptation, one can (i) compare the amount of genetic divergence of the trait in a common garden to the null expectation under genetic drift (Whitlock, 2008) or (ii) test for a correlation between the pairwise phenotypic divergence between populations in a common garden and the pairwise difference between the populations' home climates, whilst controlling for genetic similarity (Hancock *et al.*, 2011).

Transplants, by identifying the processes underpinning spatial climate-phenotype relationships, can inform as to the nature and timescale of the phenotypic response to climate change, although the space-for-time implications of transplant studies are often implicit. Where plasticity is observed, responses to climate change are expected to be immediate (Frei *et al.*, 2014; Sanginés de Cárcer *et al.*, 2017), and if conditions at transplant sites resemble those expected in the future, these immediate responses can be observed directly (Münzbergová, Vandvik & Hadincová, 2021). Conversely, where local adaptation of a trait or population to climate is detected (Leimu & Fischer, 2008; Halbritter *et al.*, 2018; Lortie & Hierro, 2021), climate change is expected to shift the optimum phenotype and place populations under directional selection to adapt over multiple generations (Etterson, 2004). In addition, transplant studies can also reveal whether phenotypic responses are lagging behind changing climate conditions (Fig. 2b): if individuals have highest fitness in environments resembling those they occupied in the past, this suggests that they are not evolving rapidly enough to keep up with the changing climate and so, are maladapted to the conditions they currently occupy (Wilczek *et al.*, 2014; Hällfors *et al.*, 2020). Another approach, originally developed for seed transfers (Campbell, 1986), is to predict the biotic offset (Fig. 2aii) of populations to future climates (termed ‘relative risk of maladaptation’) (St Clair & Howe, 2007; Frank *et al.*, 2017; Rellstab, Dauphin & Exposito-Alonso, 2021). This approach combines common garden estimates of phenotypic distributions within populations, with differences between populations, and *in situ* information on how mean phenotypes change with climate. However, this has not been widely applied in the context of climate change (Frank *et al.*, 2017). Climate transfer functions, which have been used in selecting provenances suited to future climate conditions, can also be viewed as estimates of phenotypic (in this case, fitness) offsets (Fitzpatrick *et al.*, 2021).

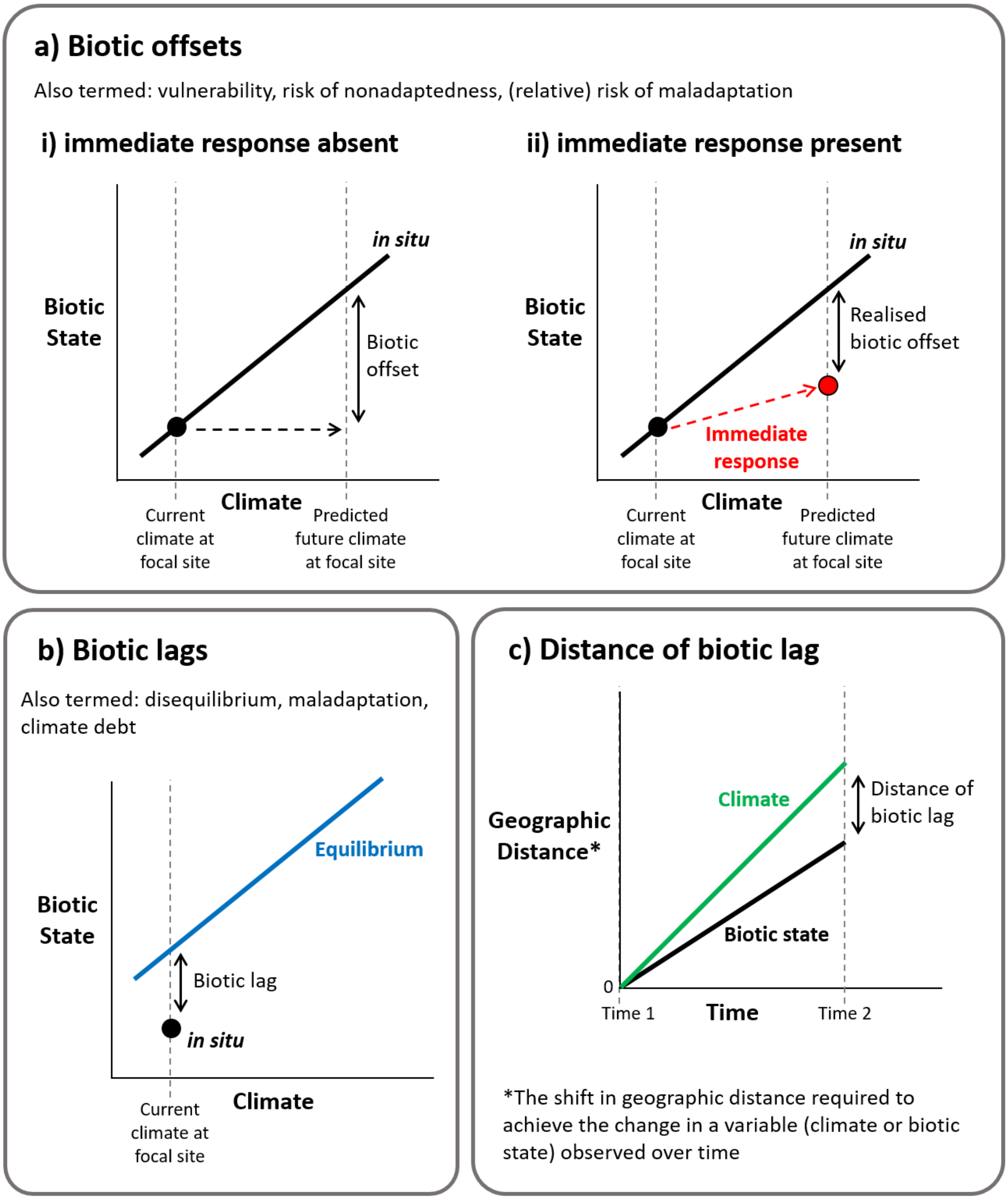

Figure 2: *Metrics of climate threat to biodiversity based on SFTS. Black circles represent a focal site. (a) biotic offsets, the distance between the current biotic state at a focal site and the predicted equilibrium biotic state at that site under future climate conditions. The current biotic state may either be (i) that observed in situ at the focal site or (ii) that accounting for an immediate response to environmental change (e.g. due to phenotypic plasticity; red circle),*

which can be observed via a common garden representing the expected future conditions (realised biotic offset). (b) biotic lags, the distance between the observed biotic state at a focal site and the predicted equilibrium state at that site under current climatic conditions. (c) where both spatial and temporal data is available, temporal shifts in both biotic states and climate variables can be quantified in terms of an equivalent shift in spatial distance, and this can be used to find the distance of biotic lag. Linear responses are depicted here for simplicity but some responses may be non-linear. Note that where the response is a species' distribution, the focus is generally on how the biotic state (presence or abundance) covaries with the environment across many populations, rather than a single population as depicted here. Where the response is species' occurrence, the biotic state can be thought of as the probability of presence.

In addition to the limitations that are general across climate-focussed SFTS methods (Table 3), there are others that are especially pertinent to inferences about population phenotypes. For instance, a particular concern for *in situ* gradient models is uncertainty regarding the relative roles of plasticity and local adaptation in shaping spatial and temporal patterns for a given trait (Boutin & Lane, 2014; Merilä & Hendry, 2014; Stamp & Hadfield, 2020). Indeed, these processes may contribute differently across spatial and temporal gradients, with the expected contribution of genetic adaptation increasing with time-scale (Dunne *et al.*, 2004). Given that geographic variation in phenotypes is known to arise via a combination of plasticity and adaptation (Franks, Weber & Aitken, 2014; Merilä & Hendry, 2014; Stamp & Hadfield, 2020), as well as their interaction (Kelly, 2019), the assumption that *in situ* gradients arise solely via one or the other process is naive. Therefore, explicit tests for local adaptation, plasticity and lags (such as via transplant studies, see above) are advisable before spatial gradients are used to predict future trait changes, but this remains rare (Keller *et al.*, 2013; Merilä & Hendry, 2014).

(2) Population genotypes

At the genetic level, *in situ* gradient approaches have provided insights into the genomic basis of climate adaptation and selection over spatial gradients (Wogan & Wang, 2018). Yet in many instances, the space-for-time inference from genetic studies is implicit (Hancock *et al.*, 2011; Waldvogel *et al.*, 2018), with only a relatively small proportion making explicit predictions regarding the impact of climate change on genotypes (Row *et al.*, 2014; Jordan *et al.*, 2017; Martins *et al.*, 2018; Exposito-Alonso *et al.*, 2018). While transplant studies are also used to study genetic markers, usually the motivation is to identify the genotypes underlying phenotype-climate associations, rather than direct associations between genotypes and climate (Fournier-Level *et al.*, 2011; de Villemereuil *et al.*, 2018; Housset *et al.*, 2018). Although, when the focus is on fitness-associated genotypes, this can be used to make inferences about climate-allele relationships (Fournier-Level *et al.*, 2011) and predictions about allele frequencies under climate change (Exposito-Alonso *et al.*, 2018, 2019).

Two main methods are applied across *in situ* gradients to identify climate-genotype relationships and the putatively adaptive loci (see VII. Glossary) suspected to be involved in local adaptation, in what is often termed landscape genomics (Schoville *et al.*, 2012; Hoban *et al.*, 2016; Li *et al.*, 2017). The first is genotype-environment association analyses, which identify climate-genotype correlations across a climate gradient (Rellstab *et al.*, 2015). The second approach involves differentiation outlier methods, which identify the loci that are most highly differentiated between different climates and so are most likely to be involved in local adaptation (where selection favours different alleles in different environments) (Hoban *et al.*, 2016). These approaches are often used in combination to increase confidence in the identification of putatively adaptive loci (Jordan *et al.*, 2017; Martins *et al.*, 2018). Both of these methods involve either (i) a candidate gene approach looking at whether specific candidate genes – which are known or suspected to be associated with a particular function that may be involved in a response to climate – are associated with climate variables (Umina *et al.*, 2005; Csilléry *et al.*, 2014; Rellstab *et al.*, 2016), or (ii) multi-marker screening which involves screening multiple regions of the genome and identifying the molecular markers (often single nucleotide polymorphisms, SNPs) exhibiting the strongest associations with climate variables (Hancock *et al.*, 2011; Bay *et al.*, 2018).

The climate-genome relationships identified across *in situ* gradients can then be used to make projections of genomic changes and selection pressures under climate change (e.g. Row *et al.*, 2014; Rellstab *et al.*, 2016; Jordan *et al.*, 2017). Recently, ecological niche modelling methods have been applied to identify climate-genotype associations from *in situ* gradients (Jay *et al.*, 2012; Fitzpatrick & Keller, 2015) or common gardens (Exposito-Alonso *et al.*, 2018, 2019) and used to predict changes in the distribution of alleles or selection pressures under future climates. Indeed, analogues of ecological niche models – which were originally used to model the distributions of species within communities – are becoming increasingly important since they can account for the multidimensionality of spatial genomic variation by modelling alleles at multiple loci in an integrated way, as with methods that model multiple species in a community (Fitzpatrick & Keller, 2015) (Section III(4)). These SFTS predictions are increasingly being used to find the biotic (genomic) offset (Fig. 2ai) (Fitzpatrick & Keller, 2015), the difference between current genetic compositions and those projected to be required under climate change, which is a more widely used analogue of phenotypic offset and variously termed genetic offset, genomic vulnerability, and risk of nonadaptedness (reviewed by (Capblancq *et al.*, 2020; Rellstab *et al.*, 2021; Hoffmann, Weeks & Sgrò, 2021). Genomic offset represents the expected level of maladaptation of a population to its future environment, and hence the amount of genetic change (i.e. adaptation) needed for the population to track the changing climate and maintain fitness.

There are two major limitation types that apply to genotypic SFTS. The first major limitation, which is unique to genotypic studies, is potential failure in identifying the causal loci underlying adaptation to climate. Multi-marker screening methods are prone to false positives when identifying putatively adaptive loci. Neutral alleles may appear to exhibit variation with an environmental variable for several reasons including demographic history, population structure, linkage disequilibrium, spatial autocorrelation, correlated environmental variables, incomplete selective sweeps, statistical bias, failure to account for multiple testing, or genotyping errors – all of which can lead to loci being incorrectly identified as involved in local adaptation (Rellstab *et al.*, 2015, 2021; Hoban *et al.*, 2016; Li *et al.*, 2017; Booker, Yeaman & Whitlock, 2021; Hoffmann *et al.*, 2021). Therefore, validation of spatial associations, ideally functional validation, is a valuable step to increase confidence that the identified associations are causal (Section IV). Multi-marker screening methods are also prone to false negatives. This can arise due to the polygenic nature of adaptation, since local adaptation often results from small changes at many loci giving rise to low power to detect each effect (Hoban *et al.*, 2016; Rellstab *et al.*, 2017; De La Torre, Wilhite & Neale, 2019; Hoffmann *et al.*, 2021). Polygenic traits also tend to have high redundancy: a single phenotype can be achieved through multiple different combinations of genotypes across loci. While redundancy increases the efficiency of local adaptation, it leads to low replicability and high turnover in the loci responsible (Yeaman, 2015), such that genotype-environment associations will only ever identify a subset of loci that could potentially aid adaptation. These difficulties are further exacerbated by sequencing methodologies that only capture part of the genome and missing structural variation (Hoban *et al.*, 2016; Hoffmann *et al.*, 2021).

The second limitation of genotype-environment associations is that the implicit assumptions of SFTS might not be met at the genotypic level. Even with perfect knowledge of the complete set of loci involved in adaptation to environment in space, we may fail to predict genotypic change over time for several reasons. First, the rate of environmental change matters: gradual change is likely to favour alleles of smaller effect, as large-effect alleles could overshoot the gradually changing optimum (Matuszewski, Hermisson & Kopp, 2015). Pleiotropy will also tend to favour adaptation through alleles of small effect (Fisher, 1930; Barghi, Hermisson & Schlötterer, 2020), especially if novel environments are not equally shifted from the present in all dimensions. By contrast, local adaptation in space is expected to involve gradual recruitment of larger effect alleles (or clusters of alleles) that are more resistant to gene flow (Yeaman, 2013, 2015). Hence, the loci with the greatest contributions to spatial adaptation in the present might not be those that are first to respond to environmental change. Another important factor is gene flow. In heterogeneous environments, adaptation may be prevented by maladaptive gene flow from nearby populations facing very different conditions (Schiffers *et al.*, 2013; Polechová & Barton, 2015). On the other hand, if gene flow is limited, local adaptation in space might not translate into an ability to adapt to climate change due to a lack of availability of suitable genetic variation where it is needed. Predictability is further reduced by the fact that adaptation can involve novel genotypes not seen over space (e.g. new mutations or combinations of alleles) (Wogan & Wang, 2018; Rellstab *et al.*, 2021). Finally, there is a broad trade-off in predictability determined by the genetic architecture of the trait under selection (Kardos & Luikart, 2021). For traits with simple genetic architecture (few loci with large individual effects and low redundancy), it is easier to predict the loci of adaptation, but there is more stochasticity in *whether* adaptation will occur (due to availability of genetic variation, pleiotropy etc.). One the other hand, for polygenic traits (many loci of small effect and high redundancy), predicting the loci of adaptation is difficult, but it is highly likely that adaptation at the phenotypic level will occur in a predictable direction.

(3) Species distributions

The most widespread use of space-for-time substitutions in climate change ecology is for anticipating how species' distributions may shift as the climate changes (Elith & Leathwick, 2009; Melo-Merino, Reyes-Bonilla & Lira-Noriega, 2020). This generally involves using ecological niche models (ENMs) (Table 1a) in which the relationships between multiple climate variables and a species' geographical distribution (occupancy, abundance) are estimated over *in situ* gradients (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Elith & Leathwick, 2009). These spatial relationships can then be projected over time to predict species' potential future distributions (Thuiller, 2004; Thomas *et al.*, 2004; Huntley *et al.*, 2008) or past distributions (Nogués- Bravo, 2009; Varela, Lobo & Hortal, 2011; Maguire *et al.*, 2015). ENMs differ from other applications of space-for-time substitutions in that they typically consider both multiple climatic drivers and non-linear spatial relationships. Given the extensive literature on the applications of ENMs (e.g. Guisan & Zimmermann, 2000; Pearson, 2010; Santini *et al.*, 2021) and that our focus is on space-for-time substitutions more generally, we only give a brief overview of how ENMs are used to project the impacts of future climate change on biodiversity.

ENMs can be used to project whether the climatically suitable area for a species will change in size, and/or shift in space under future climates, which allows predictions of species' future distributions, population trends, and extinction risks (Berry *et al.*, 2002; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Huntley *et al.*, 2008). ENMs can also be used to make inferences about biotic lags, although this concept differs slightly in the context of species' distributions because the focus is on a biotic state (local presence/absence or abundance) summarised across many populations (e.g. using distribution centroids) rather than within a single population (as shown in Figure 2). Nonetheless, a biotic lag can be inferred by projecting ENMs calibrated on past data to the present day; where distribution shifts are in the direction but not of the magnitude projected it may suggest a contemporary biotic lag (Fig. 2b) (Lewthwaite *et al.*, 2018; Soultan *et al.*, 2022). Such biotic lags can also be quantified in terms of spatial distance (distance of biotic lag; Fig. 2c; (Ash *et al.*, 2017)). A recent variation of this type of approach uses a series of hindcast ENM projections to estimate the distance of past shifts in climatically suitable areas for a species, and hence the potential migration rate, which can then be compared to the rate required under future climate change (Brodie *et al.*, 2021).

The vast majority of species-focussed SFTS rely on an *in situ* gradient approach, though there has been some limited use of transplant studies. For instance, transplants of individuals to sites either within or outside of a species' current geographical range can provide insights into the factors limiting species' ranges (e.g. climate, dispersal limitation, biotic interactions), the presence of biotic lags, and the likely responses to future climate change (Marsico & Hellmann, 2009; Willis *et al.*, 2009; Pelini *et al.*, 2009; Van der Veken *et al.*, 2012).

The limitations, assumptions and uncertainties that accompany ENM projections have been reviewed extensively (e.g. Pearson & Dawson, 2003; Sinclair, White & Newell, 2010; Peterson, Cobos & Jiménez- García, 2018; Yates *et al.*, 2018), so we focus on the assumptions made to use ENMs for SFTS projections. In particular, there is an assumption that either the realised climatic niche is conserved over time or that climate is the sole determinant of species' distributions and the species is at equilibrium with climate (Pearson & Dawson, 2003; Araújo & Guisan, 2006; Veloz *et al.*, 2012; Beale & Lennon, 2012;

Peterson *et al.*, 2018). However, the realised niche may change over time due to (i) the shift in climate not being accompanied by shifts in the other variables that limit the distribution or (ii) the emergence of new suitable climate conditions that are novel within the accessible geographic area (Pearson & Dawson, 2003; Veloz *et al.*, 2012; Beale & Lennon, 2012; Peterson *et al.*, 2018). Recent years have seen major efforts to address these issues by extending ENMs to incorporate eco-evolutionary processes (Thuiller *et al.*, 2013) such as intraspecific variation (i.e. local adaptation) (DeMarche, Doak & Morris, 2019; Garzón, Robson & Hampe, 2019; Aguirre-Liguori, Ramírez-Barahona & Gaut, 2021), demography (including dispersal and, by proxy, gene flow) (Fitzpatrick *et al.*, 2008; Fordham *et al.*, 2018), and other range-limiting factors such as biotic interactions (Araújo & Luoto, 2007; Staniczenko *et al.*, 2017; Abrego *et al.*, 2021).

(4) Ecological communities

At the community level – which we define as considering the effects of climate on more than one species simultaneously – both *in situ* gradient and transplant SFTS have been widely applied to predict biotic responses to future climate change. These have focussed on three facets of communities: (i) species composition (Nooten, Andrew & Hughes, 2014; Niu *et al.*, 2019; Kinard, Patrick & Carvallo, 2021); (ii) species interactions, including consumer-resource (Rasmann *et al.*, 2014; Tran *et al.*, 2016), competitive (Alexander, Diez & Levine, 2015), symbiotic (Steidinger *et al.*, 2019), and parasite(-vector)-host (Pickles *et al.*, 2013); and (iii) community trait (or functional type) composition (Dubuis *et al.*, 2013; de Oliveira *et al.*, 2020). Community-focussed SFTS are extensions of species-focussed SFTS (community composition and species interactions) and phenotype-focussed SFTS (community traits), the difference being the consideration of multiple species. Therefore, many of the same inferences and limitations are relevant.

In situ gradient methods are widely used to make community-level SFTS projections (Meerhoff *et al.*, 2012; Dubuis *et al.*, 2013; Mokany *et al.*, 2015; Newsham *et al.*, 2016; Kwon *et al.*, 2019; de Oliveira *et al.*, 2022). This includes the frequent use of ENM methods which, at the community level, involve three main approaches (Ferrier & Guisan, 2006; Nieto-Lugilde *et al.*, 2018): (i) modelling the association of climate with a community-level attribute, such as grouping species into vegetation classes (Hilbert & Ostendorf, 2001; Pearson *et al.*, 2013); (ii) modelling individual species' responses and overlaying their potential distributions under climate change to make community-level inferences (stacked models) (Thuiller *et al.*, 2006; Gallagher, Hughes & Leishman, 2013; Davis, Champion & Coleman, 2022); or increasingly, (iii) simultaneously modelling multiple species' distributions to allow for reciprocal interactions, often termed joint species distribution modelling (JSDM) (Pollock *et al.*, 2014; Tikhonov *et al.*, 2017), though the focus of this approach can be on either the community or the constituent species.

Where transplants are used to make SFTS inferences at the community level, this has involved either: (i) moving a single species into a new environment, thus mimicking the novel species interactions that may occur as species' distributions and phenologies shift under climate change (Andrew & Hughes, 2007; Heimonen *et al.*, 2015); (ii) moving multiple species into different environments to provide insights into potential community responses to future climate change, either by directly moving species (De Block *et al.*, 2013; Nooten *et al.*, 2014; Descombes *et al.*, 2020) or by transplanting soil cores containing microbial communities and/or seed banks (Budge *et al.*, 2011; Tomiolo, Bilton & Tielbörger, 2020); and (iii) a combination of (i) and (ii) (Alexander *et al.*, 2015).

In addition to generating predictions of community-level changes under climate change, SFTS can provide insights into the processes generating spatial patterns and thus potentially involved in responses to future climate change. The community trait compositions observed across *in situ* gradients may result from a combination of climate-driven changes in species turnover and/or intraspecific processes (i.e. plasticity and genetic differentiation; Section III(1)). The relative contributions of interspecific and intraspecific processes can be disentangled by comparing how a climate gradient explains spatial variation in (i) community trait means calculated across all individuals of all species, which result from a combination of interspecific and intraspecific trait variation, and (ii) species-weighted community trait means, which represent interspecific variation alone (Lajoie & Vellend, 2018). The contributions of intraspecific genetic and plastic processes to climate-induced community changes can also be separated using transplants (Garibaldi, Kitzberger & Chaneton, 2011; Lajoie & Vellend, 2018) (Section III(1)), but with the added complexity that biotic responses may be affected by interacting species as well as climate.

Where temporal and spatial data are available, inferences can also be made about the presence of a lag in the temporal community response to climate change (Fig. 2b), using the same approaches as for phenotypes (comparing spatial and temporal climate-biotic response slopes (Sandel, 2019; Gaüzère *et al.*, 2020); Section III(1)) or species distributions (comparing current observations to predictions based on historically-calibrated models (Menéndez *et al.*, 2006); Section III(3)). These lags can also be quantified in terms of geographic distance (Distance of biotic lag, Fig. 2c; (Devictor *et al.*, 2008, 2012)).

SFTS at the community level are subject to similar limitations as when looking at species (Section III(3)) and phenotypes (Section III(1)). However, there are also additional limitations that arise when considering multiple species together. Under climate change, different species may shift their distributions and phenologies in different ways, resulting in complex changes in community compositions and biotic interactions (Beissinger & Riddell, 2021).

Given the uncertainties regarding how each species will respond to future climatic shifts, communities may change in ways that are unanticipated on the basis of contemporary *in situ* gradients and transplant experiments. Alternatively, it is possible that emergent community responses are more predictable if consideration of multiple species averages away some of the stochasticity in individual species' responses.

Community-focussed transplants tend to involve (i) a subset of species from a community, which is often taxonomically biased due to the logistics of moving species, and (ii) a relatively small number of individuals of each species, despite the fact that population size can impact community outcomes such as species interactions (Morton & Rafferty, 2017). Furthermore, while inadequate spatial replication is a common issue with all transplant experiments, this is particularly pronounced for community-focused studies due to the logistical challenges of moving multiple species. In fact, it is common to see climate variation represented by just two or three sites (e.g. Alexander *et al.*, 2015), such that it is impossible to isolate the causal environmental variable.

IV. Validation of SFTS

Across all subfields, the performance of climate change SFTS has been found to be mixed, with studies both supporting (e.g. Blois *et al.*, 2013; Banet & Trexler, 2013) and contesting (e.g. La Sorte *et al.*, 2009; Isaac *et al.*, 2011; Wu *et al.*, 2022) the use of SFTS, and performance varying across different biotic responses and systems (e.g. Dobrowski *et al.*, 2011; Bjorkman *et al.*, 2018).

Two types of validation are needed when a SFTS projection is made. First, we need to validate that the climate predictor(s) is/are causal, which we term spatial validation (Table

3a). Typically, this involves using either non-independent spatial data (e.g. data splitting), independent spatial data from a different location (replication) or experiments (including transplants or lab studies). Where there has been spatial validation this increases confidence that the identified drivers are important in space, but it does not test transferability. The second validation type, which we term SFTS validation, involves comparing spatial model relationships or SFTS projections with temporal relationships or temporal data. Assuming that causal relationships have been estimated in space, then the SFTS validation tests the central assumption of space-time equivalence (Table 3b). Different types of data can be used for SFTS validation, including from historic long-term monitoring (La Sorte *et al.*, 2009; Rapacciuolo *et al.*, 2012), museum or herbarium collections (Guerin, Wen & Lowe, 2012), paleodata such as pollen records or fossils (Blois *et al.*, 2013), dendrochronology (Klesse *et al.*, 2020), genomics (Miller *et al.*, 2021), and *in silico* (Qiao *et al.*, 2019). When conducting SFTS validation, the timescale is an important, yet often overlooked, consideration since SFTS predictive accuracy will often be sensitive to whether projections are for the long or short term (Table 3bii) (Petchey *et al.*, 2015; Adler, White & Cortez, 2020). Note that testing for biotic lags (Fig. 3b) – which generally involves comparing temporal climate-biotic responses to those expected based on spatial associations – is a type of SFTS validation, where one can observe if the response is in the correct direction, with additional inferences made about the biotic state lagging behind the equilibrium state.

Ideally, both spatial and SFTS validation should be conducted alongside any use of SFTS. However, a lack of long-term temporal data has meant that most validation has been conducted in space alone. Below, we consider how validation has been conducted in each subfield and highlight issues.

(1) Population phenotypes

Neither spatial nor temporal validation is common practice when analysing correlative climate-biotic relationships across *in situ* phenotypic gradients or transplant experiments, which may be attributable to the exploratory nature of many analyses, funding, time and logistical constraints, or perhaps simply oversight. An indication that spatial relationships are causal could be obtained using meta-analyses, replication across multiple gradients or gradient types, or experimental manipulation of climate. There are a handful of instances of SFTS validation using historical data (Hodgson *et al.*, 2011; Guerin *et al.*, 2012; Jochner, Caffarra & Menzel, 2013) and repeated experiments (Bradshaw & Holzapfel, 2001). Space-time comparisons have also been used to assess the extent to which spatial associations are transferable over time (Table 1aii; Phillimore *et al.*, 2010, 2012; Kharouba *et al.*, 2014; Klesse *et al.*, 2020; Wu *et al.*, 2022).

(2) Population genotypes

Where validation has been conducted at the genotypic level, it has typically focussed on spatial validation rather than SFTS validation. Spatial validation is often assessed by using multiple approaches to identify putatively adaptive loci – both genome-environment association and differentiation outlier methods, or tests for genetic signatures of past selection – to increase confidence that identified loci are involved in local adaptation (Jordan *et al.*, 2017; Martins *et al.*, 2018; Exposito-Alonso *et al.*, 2019) and there are cases where a locus shows parallel adaptation to climate in different regions (Umina *et al.*, 2005). Alternatively, direct functional validation of fitness effects can be obtained experimentally to provide a more direct link between alleles and fitness under particular conditions. This has been done using transplants (Hancock *et al.*, 2011; Jaramillo-Correa *et al.*, 2015; Faske *et al.*, 2021) and there is also potential to utilise genetic modifications (e.g. knock-outs, gene transfers, or gene editing; Li *et al.*, 2017). Similarly, SNPs associated with high fitness in a common garden environment can be validated by observing whether they are more abundant in areas with climates that are more similar to the common garden (Fournier-Level *et al.*, 2011; Exposito-Alonso *et al.*, 2019). As well as validation of the loci involved in adaptation, transplants have also been used to validate genomic offset predictions by looking for associations between these predictions and performance in the corresponding common garden environment (Fitzpatrick *et al.*, 2021).

There have been few tests of whether the same loci are correlated with climate variables over space and time (but see Umina *et al.*, 2005; Balanyá *et al.*, 2006), presumably due to a lack of suitable long-term genetic data. Indirect SFTS validation of genomic offset predictions can be made by comparison with data on population trends from surveys (Bay *et al.*, 2018), or by measuring proxies for fitness in the wild (Borrell *et al.*, 2020).

(3) Species distributions

Validation of species distribution-focussed SFTS typically involves spatial validation only; this sometimes involves spatially independent data (Randin *et al.*, 2006; Early & Sax, 2014) or transplants (Willis *et al.*, 2009; Dixon & Busch, 2017; Merlin, Duputié & Chuine, 2018; Greiser *et al.*, 2020), but most often validation is conducted using non-independent data which can lead to underestimates of parameter uncertainty (Araújo *et al.*, 2005; Santini *et al.*, 2021).

Underlying an ENM prediction of a species' geographic distribution is a description of its niche in terms of response curves for each climate variable and rankings of the importance of each variable; these estimates represent an additional, underutilised opportunity for spatial validation (Buermann *et al.*, 2008; Convertino *et al.*, 2012; Searcy & Shaffer, 2016; Mothes *et al.*, 2019). This involves either (i) comparing the observed and predicted occurrence probabilities for each climate variable's response curve (Buermann *et al.*, 2008;

Convertino *et al.*, 2012) or (ii) comparing response curves and/or variable rankings to independent data on physiological tolerance (Searcy & Shaffer, 2016; Mothes *et al.*, 2019), population dynamics (Thuiller *et al.*, 2014) or simulations (Smith & Santos, 2020) to increase confidence that identified associations are causal. However, as far as we are aware, very few studies have used these underlying metrics to assess ENM performance in the context of climate change projections (Searcy & Shaffer, 2016).

SFTS validation of ENMs has been limited to use of historic datasets (Araújo *et al.*, 2005; Pearman *et al.*, 2008; Dobrowski *et al.*, 2011; Rapacciuolo *et al.*, 2012; Brun *et al.*, 2016; Morán-Ordóñez *et al.*, 2017), simulations (Beale, Lennon & Gimona, 2008; Qiao *et al.*, 2019), comparisons of predictions made using spatial data and time series data (Isaac *et al.*, 2011) or space-time comparisons (Oedekoven *et al.*, 2017; Bradter *et al.*, 2022).

(4) Ecological communities

As with species, spatial validation of community-focussed ENMs usually involves non-independent data (Norberg *et al.*, 2019). Community transplants can also be used to validate *in situ* gradient approaches, by exploring whether species' relative abundances in a common garden environment correspond to those expected based on the climate-trait relationships observed across an *in situ* gradient (Guittar *et al.*, 2016). As far as we are aware, spatial validation for species interaction-focused SFTS is lacking.

SFTS validation of changes in community compositions and traits has been assessed using historical data (Lemoine, Schaefer & Böhning-Gaese, 2007; Algar *et al.*, 2009; Blois *et al.*, 2013; Maguire *et al.*, 2016; Bjorkman *et al.*, 2018). Another approach for assessing SFTS validation has involved a comparison of the spatial and temporal relationships between climate and community traits (La Sorte *et al.*, 2009; Elmendorf *et al.*, 2015; Sandel, 2019;

Gaüzère *et al.*, 2020) or community composition (Lemoine & Böhning-Gaese, 2003; White & Kerr, 2006; Adler & Levine, 2007; La Sorte *et al.*, 2009). Similarly, warming and water addition experiments have been used to validate *in situ* gradient SFTS for species interactions (Kazenel *et al.*, 2019) and trait compositions (Sandel *et al.*, 2010).

(5) Feasibility and logistics of SFTS validation

Both spatial and SFTS validation are essential for ensuring the accuracy of projections, yet validation has been strikingly scarce. In some cases, such as SFTS validation for species distributions, validation may be logistically challenging because of the long timescales involved. However, in many cases, the lack of validation is likely due to the constraints of resources and funding rather than a lack of feasibility, since validation requires the acquisition of additional spatial data (spatial validation) or temporal data (SFTS validation). Given that validation is a vital step for generating meaningful predictions, a greater emphasis should be placed on ensuring that models can be validated.

V. Opportunities for SFTS

Given the urgency imposed by rapid anthropogenic global change, SFTS is a vital tool for predicting ecological and evolutionary responses to a changing climate. However, its value will depend on the robustness of its predictions. Here, we consider some of the major ways in which SFTS reliability could be improved, with an emphasis on how approaches and methods could be transferred between subfields; see Table 3 for a more comprehensive overview of how the major limitations of SFTS may be addressed.

A major challenge shared by all SFTS is identifying causal climate-biotic relationships (Table 3a). This issue is especially acute for transplant studies, with most considering only a single transplant site and few source populations (Johnson *et al.*, 2021) and thus lack power to detect a causal climate-biotic relationship. One way to address this is to increase replication across sites, climate gradients and gradient types (e.g. altitudinal and latitudinal) to a level that provides adequate statistical power.

A related issue is selecting putatively causal environmental variables, and there are approaches used in some subfields that could be applied more widely. For example, ENMs, which are usually applied to species or communities, are unique in the fact that they commonly consider multiple climate variables and nonlinear climate-biotic associations. On the other hand, some phenotype-focused studies focus on identifying the seasonal period over which an environmental variable is important using approaches such as sliding-windows (van de Pol *et al.*, 2016) and penalised signal regression (Roberts, 2008).

The other major challenge across SFTS is validating temporal transferability (Table 3b). An underutilised avenue for validation lies with historical data: SFTS hindcasts can be validated against the past or calibrated on past data and validated against the present (Dobrowski *et al.*, 2011; Maguire *et al.*, 2015). Additionally, there is clear value in the greater use of simulations to examine the accuracy and precision of projections under different hypothetical scenarios and thus the limits to inference. Powerful methods for realistic genome evolution now make this particularly feasible for testing inference at the genomic level (Haller & Messer, 2019; Láruson *et al.*, 2022). While many studies project biodiversity responses to distant time horizons (e.g. the end of the century), near-term forecasts provide a means of validating metrics of change (Slingsby, Moncrieff & Wilson, 2020), although this will only capture short-term responses and so may overestimate long-term predictability. Finally, as well as validating SFTS predictions for a single point in time, comparison of spatial and temporal climate-biotic response slopes (space-time-comparison, Table 1aiii) could be applied more widely for SFTS validation and to provide further insights into (i) how SFTS predictive accuracy and biotic offsets vary with timescale of projection and (ii) the processes that give rise to spatial climate-biotic relationships.

Dynamic process-based models also offer considerable potential for projecting responses over time. In such models, responses are iterated forwards through time constrained by empirically estimated parameters describing rates of key ecological or evolutionary processes (Morin, Augspurger & Chuine, 2007). However, many biodiversity projections are instead based on a static ‘snapshot’ approach, where the SFTS model is projected forwards in a single step using the climatic conditions averaged over some future often remote time period. As a result, an important aspect of temporal transferability of SFTS relates to whether current biotic responses are at equilibrium with the environment and to the timescale of projection.

If current biotic associations are at equilibrium, then SFTS based snapshot projections will indicate the future biotic response expected at equilibrium. In contrast, if current biotic associations are not at equilibrium, and are lagging behind recent warming, then future snapshot projections would underestimate the magnitude of the biotic response expected at equilibrium. However, this does not necessarily invalidate SFTS projections as these may still reliably indicate the magnitude of the *transient* biotic response, depending on whether the biotic lag is constant or changing over time. Specifically, if the biotic lag is constant over time, then projections would still be expected to reliably indicate the magnitude of the transient biotic response. On the other hand, if the biotic lag is growing over time, due for instance to accelerating climate change, then projections would underestimate the magnitude of the transient biotic response. An important avenue for research is therefore to quantify lags in biotic responses and how these may be expected to change over time. For example, ENMs typically use historical averages of climate predictors (e.g. 30 year averages from WorldClim; Fick & Hijmans, 2017), but a sliding window approach could be applied to identify the decadal period over which historical climates best predict the current state of the system, which may provide an opportunity to identify biotic lags. Similarly, when making projections of future biotic responses, annual resolution climate data from climate models can be used to project how biotic offsets may accumulate dynamically over time, providing an indication of the rate, timing and abruptness of expected responses that is not provided by static snapshot projections (Trisos, Merow & Pigot, 2020).

A related issue, is the timescale over which future projections are made and how they are used and interpreted. Low SFTS predictive accuracy may be due to mismatches between the timescale of projections and the timescale of the processes driving biotic responses (Adler & Levine, 2007; Elmendorf *et al.*, 2015; Münzbergová *et al.*, 2021). However, relatively few studies have directly explored how timescale affects SFTS performance (e.g. Roberts & Hamann, 2012; Blois *et al.*, 2013; Morán-Ordóñez *et al.*, 2017; Adler *et al.*, 2020; Bradter *et al.*, 2022). Addressing this represents an important avenue for future work, with the potential to utilise historical or *in silico* data. In addition, any assessment of SFTS performance will depend on what exactly we are trying to predict. For example, ENMs may be able to reliably identify those populations that will be exposed to unsuitable climates under a given magnitude of warming, but predicting the biotic response to exposure is more challenging because this is likely to depend on when in the future exposure occurs and thus the capacity for processes such as adaptation to rescue populations. In some cases, projections of exposure may be sufficient to provide a reliable indicator of the magnitude of climate risk across geographic space or species. If, however, the aim is to provide a reliable indication of the biotic response to exposure, then studies would benefit from considering the temporal aspect of climate change more explicitly by using process based models, or at least dynamic projections of climate change, rather than static snapshots. Genomic studies can also be improved by greater clarity on what we are trying to predict. Unlike ENMs, genotype-environment associations are only informative about the *relative* fitness of different genotypes in a given environment, and do not reveal the more important measure of *absolute* fitness (which crucially tells us whether the population growth rate will become negative in a given environment). Steps in this direction include using direct measures of fitness in the wild (Borrell *et al.*, 2020).

From examination of the tools used in different subfields it is evident that greater communication amongst subfields could benefit progress. In some cases, different subfields have developed equivalent tools independently and this is particularly evident in the case of what we have termed biotic lags and offsets (Fig 2). However, the opportunities to readily identify these parallels may have been reduced by each subfield adopting its own terminology. One of our hopes from this review is that by emphasising the similarities of aims, tools, limitations and challenges across subfields that this will foster greater communication and exchange of ideas.

VI. Conclusions

1. SFTS is currently very widely used across subfields as a pragmatic tool for generating urgent temporal predictions of biotic responses to global change. Across subfields there are many similarities in the approaches used, their strengths and their weaknesses.
2. The limitations that are common across subfields and can undermine robustness of inference are in correctly detecting causal relationships and in transferability of

spatial relationships over time. We identify opportunities and best practice to improve the reliability of SFTS.

3. We identify several instances where equivalent approaches go under different names in different subfields, highlighting the value of increased cross-talk between subfields and recognition of parallels.
4. We also identify some methods that are used effectively in some subfields, but could be used in others.
5. We anticipate that in the near-term SFTS will remain one of the major approaches to projecting future biotic responses to global change. Therefore, we strongly encourage engagement with development of new methods and protocols that can address the limitations we identify and increase the value of projections.

VII. Glossary

Biotic lag: the biotic distance (e.g. Euclidian distance between phenotypic trait values) between the observed (or predicted) biotic state under specific climate conditions and the predicted equilibrium state for those conditions (Fig. 2b). Also termed maladaptation, mismatch, disequilibrium, and climate debt.

Biotic offset: the biotic distance (e.g. Euclidian distance between phenotypic trait values) between the current state of a biotic response at a focal site and the predicted equilibrium state at this site under future climatic conditions (Fig. 2a) (Fitzpatrick & Keller, 2015; Frank *et al.*, 2017). This may account for an immediate response to environmental change (realised biotic offset). Also termed vulnerability, risk of nonadaptedness, (relative) risk of maladaptation.

Biotic response: a change in a biotic state that is driven by a change in climate. In this paper the main biotic variables we discuss are population phenotypes, population genotypes, species' distributions and communities.

Biotic state: The value of a biotic variable under particular climate conditions.

Climate-biotic relationship: the correlation between climate variables and a biotic response in space or time.

Common garden: organisms (i.e. individuals or communities) are moved into the same environment (Figure 1b, Table 1bi).

Distance of biotic lag: a biotic lag quantified in terms of spatial distance (Figure 2c, Table 1aiii). Where spatial and temporal data are both available, changes in a biotic response and climate over time can each be quantified in terms of a shift in spatial distance. The difference between these shifts is the distance of biotic lag (Devictor *et al.*, 2008, 2012). Also referred to as a spatial lag.

Ecological niche model (ENM): a group of *in situ* gradient methods aiming to correlate the distribution of a biotic response (usually a species' presence/absence) with one or more environmental variables in order to predict environmental suitability for the response across a landscape and under altered conditions. There are various other terms for ENMs including environmental niche models, species distribution models, (bio)climate envelope models, and habitat suitability models (Peterson & Soberón, 2012; Araújo & Peterson, 2012).

Equilibrium: a biotic state that is stationary in relation to its environment, where the effects of countervailing processes are in balance (Coulson, 2021). There may be multiple stable equilibria for a biotic response (Chase, 2003).

***in situ* gradient approach:** spatial climate gradients are used to identify climate-biotic relationships (Figure 1a, Table 1a). This includes ecological niche models.

Local adaptation: where spatially variable environments impose selection that maintains genotypic differences between locations, such that the fitness of individuals tends to be greater than foreign individuals in their home conditions than in other conditions.

Phenotypic plasticity: where a genotype gives rise to different phenotypes under different environmental conditions.

Putatively adaptive loci: loci identified as potentially being involved in local adaptation. These loci exhibit associations with climate, but correlative methods do not prove that they are causally involved in local adaptation.

Reciprocal transplant: organisms (i.e. individuals or communities) from different sites are moved into each other’s environments so that the performance of local and foreign organisms at a site can be compared (Figure 1c, Table 1bii).

Space-for-time substitution (SFTS): spatial climate-biotic correlations are used as a substitute for temporal correlations to make inferences about biotic changes over time (Pickett, 1989). Note that here our focus is on climate-biotic associations but SFTS are also applied to other drivers and responses.

Space-time comparison: climate-biotic relationships are separately estimated over space and over time. Comparison of these associations can provide insights into the processes generating these spatial and temporal associations (Table 1aii). Note that this has an implicit SFTS since the spatial climate-biotic relationship is assumed to capture the equilibrium association.

Space-time equivalence: spatial and temporal data are utilised together with an assumption that climate-biotic associations in space and time are equivalent.

Transplant experiments: organisms (i.e. species or communities) are moved from a home site into different environments over space (away sites) (Table 1b). Transplants may be common gardens or reciprocal transplants.

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Table 1: Space-for-time and space-time comparison methods used in climate change ecology and evolution to study biotic responses including population genotypes and phenotypes, species distributions, and ecological communities.

Method		**Purpose and Inference**	**Limits to inferences**
(a) ***In situ*** **gradients (regression) including ecological niche models (ENMs)** Use of spatial climate gradients (e.g. latitudinal,	**(i) SFTS with a single or multiple predictor(s)** Estimate the correlation between one or more climate variable and a biotic response over space to make projections over time.	1. Climate-biotic relationships are assumed to capture causal effects, under the assumption that there are no third variables. Estimate can then be used to project biotic responses to a change in the focal climate variables over time. 2. Where multiple climate variables are considered, it is possible to infer the relative importance of different variables as predictors of a biotic response.	1. Does not prove a causal effect of climate variables on the biotic response and the relationship is sensitive to third variables. 2. Silent on the mechanisms of the biotic response to the climate predictors in space and whether the response manifests over short or long-timescales. 3. Assumes that current spatial patterns reflect the equilibrium (or in special cases

altitudinal) to identify associations between climate variables and biotic responses (Fig. 1a).			optimum) association between the focal climate predictors and the biotic response.
	(ii) Space-time comparison Estimate the effect of climate on the biotic response separately over space and over	1. Where the slope of the relationship between a climate variable and the biotic response is in the same direction over space and time and similar in magnitude, this is consistent with climate having a causal effect and implies that spatial estimates are transferable to a temporal context (i.e. it is a form of SFTS validation – see section IV).	1. Particularly sensitive to third variables, as both the spatial and the temporal slopes may be affected (Tansey *et al.*, 2017), meaning that particular caution is recommended when drawing inferences.

	time and compare the direction and magnitude of the slopes. The spatial climate-biotic response is often assumed to capture the equilibrium (or in special cases the optimum) relationship.	2. Where spatial and temporal climate-biotic slope estimates differ in direction or magnitude, this may suggest that different processes are operating over space and time. Where slopes differ in direction or one of the relationships is non-significant, this reduces confidence that the climate variable is causal. 3. Spatial relationships are often assumed to capture the equilibrium (and in special cases the optimum) response. Therefore, where spatial and temporal climate-biotic slopes are in the same direction but steeper over space than over time, this can reveal the presence of a contemporary biotic lag or a biotic offset under a future climate.	2. Assumes that current spatial patterns reflect the equilibrium (or in special cases optimum) association between the biotic response and the focal climate predictors.

	(iii) Quantifying temporal change as distance Estimating the change in a variable (i.e. climate or biotic state) over a spatial gradient (e.g., latitude) and over time allows a temporal change to be translated into the spatial distance over which the equivalent change in the variable is observed.	1. When applied to climate data alone this approach can be used to quantify local climate velocity (Loarie *et al.*, 2009), which is a vector of the distance in space that provides an equivalent shift in climate to the change observed over time. 2. A temporal biotic lag can be quantified in terms of spatial distance by finding the difference between the spatial shift in climate and the spatial shift in a biotic response in a focal time period (Fig. 2c). This 'distance of biotic lag' metric has the benefit of units (e.g. km) being easily interpretable and allowing multiple biotic responses to be compared on the same axis.	As above

(b) Transplants Moving organisms into different environments over *space* to provide insights into their responses to environmental change that may occur over *time.*	**(i) Common gardens (SFTS)** Organisms from two or more different sites are moved into a shared environment (Fig. 1b). This can either be done *in situ* along an environmental gradient and/or in an experimentally manipulated environment. Comparison between	1. Comparing biotic state at a home site to that at away (transplant) sites can reveal an immediate response to environmental change (e.g. plasticity). The immediate biotic responses to a climate driver can be estimated where (i) the climate variable(s) is/are manipulated across replicates or (ii) replication of source sites permits statistical analysis of causal effect of climate variables. 2. Comparing the performance of organisms from different sites of origin within a common environment can inform about persistent differences between sites (e.g. genetic differentiation).	1. Where replication is insufficient (i.e. a limited number of sites are considered) and climatic conditions are not manipulated experimentally, common gardens do not inform on the effects of specific climate drivers on biotic responses. 2. Among organism differences in a common garden environment are not sufficient on their own to evidence spatial differences in equilibrium biotic state (e.g., local adaptation).

	organisms originating from different locations can provide the basis for space-for-time inference.	3. Where a transplant climate is representative of historical conditions, this can inform regarding biotic lags: if performance (e.g. fitness) is higher in climates resembling those occupied in the past, it may suggest that the biotic state is lagging behind the changing environment. 4. When the conditions within a common garden (away site) are representative of the future conditions expected at the home site, predictions can be made about the expected responses to future climate change, assuming that climate is causal. This includes estimating biotic offsets (Fig. 2a).	

	(ii) Reciprocal transplants (sometimes called reciprocal common gardens) (SFTS) Organisms from different sites are moved into each other's environments allowing the performance of local and foreign organisms at a site to be compared (Fig. 2c).	1. Comparing biotic states in home sites to that at away (transplant) sites can reveal an immediate response to environmental change (e.g. plasticity). 2. Comparing the performance of organisms from different sites of origin within a common environment allows quantification of persistent differences between sites (e.g. genetic differentiation) with respect to the environment. Since reciprocal transplants involve maintaining organisms in both local and foreign sites – such that native and foreign performance can be compared – they allow these persistent differences in performance (but not other aspects, e.g., phenotypes) to be attributed to spatial	1. Where replication is insufficient (i.e. a limited number of sites are considered), reciprocal transplants cannot reveal which aspects of the environment (including climate) drive responses. 2. For populations/communities at range margins reciprocal transplants cannot inform about biotic lags with respect to environmental change since they only involve sites within the current range of a biotic response.

		differences in the equilibrium or optimum biotic state (e.g., local adaptation; Kawecki & Ebert, 2004)). 3. Where a transplant climate is representative of historical conditions, this can inform regarding biotic lags: if performance (e.g. fitness) is higher in climates resembling those occupied in the past, it may suggest that the biotic state is lagging behind the changing environment. 3. Where replication (i.e. the number of sites) is sufficient, reciprocal transplants allow (1) and (2) to be estimated with respect to a specific climate driver.	

		4. When the conditions within an away (transplant) site are representative of the future conditions expected for a focal home site, predictions can be made about the expected responses to future climate change, assuming that climate is causal. This includes estimating biotic offsets (Fig. 2a).	

Table 2: Example papers using space-for-time substitutions for each of the eco-evolutionary subfields covered in this paper (population phenotypes, population genotypes, species' distributions, ecological communities). Papers were selected to demonstrate the breadth of SFTS methods, applications and inferences.

Subfield	**Example paper and SFTS method(s) used**	**Summary**
(a) Population phenotypes	**Wilczek *et al.* 2014** ***PNAS*** Reciprocal transplants Inferring biotic lag	Wilczek *et al.* transplanted seed bank accessions of *Arabidopsis thaliana* collected across four European regions into each of four common garden sites across the species' European range (Spain, the UK, Germany and Finland). They estimated the fitness (based on fecundity) of different genotypes at different sites. On a broad scale, genotypes with origins near to each common garden site had higher relative fitness than those from other regions, suggesting the presence of local adaptation. However, for the most northerly site in Finland they found that accessions originating from a historically warmer location had higher fitness than the home accessions, consistent with the historically collected accessions from this region exhibiting adaptational lag.

(b) Population genotypes	**Bay *et al.* 2018 *Science*** *in situ* gradient Estimating biotic offset	Bay *et al.* characterised more than 100,000 SNPS from breeding populations of yellow warbler, *Setophaga petechial*, sampled across 21 locations in North America. They examined the spatial genotype-environment association for each SNP across a range of climate and environmental variables (with climate, vegetation indices, tree cover, elevation and surface moisture). These contemporary associations were then used to predict SNP values for a particular climate model for 2050. Geographic variation in predicted genomic vulnerability (i.e. biotic offset) was calculated as the Euclidean distance between contemporary and predicted SNPs. The authors found that regions with higher genomic vulnerability had already experienced the largest population declines, suggesting that these populations are already being negatively affect by climate change.
(c) Species distributions	**Thomas *et al.* 2004 *Nature*** *in situ* gradient (Ecological niche models, ENMs)	Thomas *et al.* fitted separate ENMs for 1,103 terrestrial animal and plant species, based on the climate conditions they currently occupy. They used these contemporary associations to project species' distributions under projected climate change for 2050. Based on the predicted area loss, the authors then estimated the proportion of species expected to go extinct under different climate-warming scenarios. They estimated that

		between 9% and 52% of species would be ‘committed to extinction’, depending on the climate and dispersal scenario, highlighting the importance of minimising climate warming.
(d) Ecological communities	**Alexander *et al.* 2015** ***Nature*** Common garden transplants	Alexander *et al.* transplanted both (i) four focal plant species and (ii) intact alpine plant communities to two sites on an elevational gradient in the Swiss Alps. Transplants simulated different migration scenarios that may occur under climate change, such that each focal species experienced different combinations of (i) current or warmer temperatures and (ii) current or novel communities. Novel competitors reduced performance of plants under increased temperatures (i.e. migration failure) but had little effect under current temperatures (i.e. climate tracking).

Table 3: General limitations of SFTS that apply across all subfields and potential ways to address these issues

Limitation category	**Limitation**	**Improvements and Recommendations**
a) Causality Issues identifying causal associations	**i) Identification of causal climate predictors** Both the omission of causal predictors and inclusion of redundant predictors (i.e. overfitting) can bias SFTS estimates (Synes & Osborne, 2011; Beale & Lennon, 2012). Omitted causal variables could be other abiotic or biotic variables and their non-inclusion reduces our ability to accurately predict responses in time. It may also lead to correlated but non-causal variables being identified as important predictors, though with a weaker effect than the true causal variable would have (Dormann *et al.*, 2013). Omitted causal variables are especially problematic for SFTS	1) Choosing variables that are likely to be causal based on biological knowledge. 2) Where climate-biotic slope estimates are similar across multiple gradients or types of gradients (e.g. altitudinal, latitudinal, urbanisation), this can increase confidence relationships have a causal basis. 3) Estimating the correlations between multiple abiotic (including climate) and biotic variables in space versus time would provide us with an insight into how often and where differing correlations are likely to pose a challenge to predictions (Dormann *et al.*, 2013).

	where correlations between the causal and non-causal variable differ in space and time (Tansey *et al.*, 2017). Causal inference may also be problematic in experiments. In transplant experiments, the challenges of 'excludability' (where the treatment has other unintended consequences) and 'noncompliance' (where the treatment climate that a transplant experiences cannot be fully controlled) may be particular challenges (Kimmel *et al.*, 2021). Problems with inferring causality are likely to be most pronounced where replication is insufficient.	4) There are approaches for choosing drivers that could be shared between subfields. For example, phenotypic studies often focus on the seasonal timing over which a predictor is important (Roberts, 2008; van de Pol *et al.*, 2016), whereas ENMs generally consider multiple climate variables and nonlinear climate-biotic associations.
	ii) Sampling issues A spatial sample may not capture the true association between variables, such as due to sampling biases or	1) Selective sampling of environments, such as stratified sampling or matching methods (Andam *et al.*, 2008), could

	incomplete sampling. Additionally, if there is variation in the availability of different climate conditions over space, this may result in unequal representation in the sample.	be used to generate a sample that is representative of the available climate conditions. 2) A greater emphasis could be placed on statistical power in study design.
	iii) Spatial autocorrelation Spatial autocorrelation is ubiquitous in biotic and climatic data, with sites that are closer together having more similar values. This means that spatial samples will often not be independent and this leads to inflated confidence in model estimates (Dormann, 2007).	1) Modelling methods that address spatial autocorrelation in the residuals do now exist and are getting faster and more able to deal with large and complex datasets, e.g., INLA (Rue, Martino & Chopin, 2009). 2) For genomic data, where spatial proximity may lead to greater genetic similarity via isolation by distance, methods have been developed to try to capture and control for relatedness between populations (Reviewed by Rellstab *et al.*, 2015).

	iv) Spatial scale Generally, associations between climate and a response are modelled using relatively coarse grain predictors (e.g., estimates for 100, 10 or 1km^2; (Fick & Hijmans, 2017)), which may not be representative of the local conditions that drive a biotic response (Potter, Arthur Woods & Pincebourde, 2013). This can introduce measurement error variance into our climate predictors, which will bias slope estimates toward zero. Climate-biotic slope estimates can also be biased away from 0 where there is a tendency for biotic responses to use less extreme microclimates as one moves toward more extreme climates. For example, microclimates can provide suitable climatic refugia for a biotic response, even when coarser scale climate conditions would render a site unsuitable	1) Where interpolated climate data are used we recommend using the finest scale available, depending on suitability to the biotic response (Suggitt *et al.*, 2017). 2) Where the biology of the system suggests that microclimates are likely to be important, we recommend that microclimatic modelling (Kearney *et al.*, 2020; Maclean, 2020) is used to arrive at climate predictors (Stark & Fridley, 2022). 3) If microclimates are changing in the same way as coarser climate variables over space and over time, this may not affect space-for-time predictions. Therefore, we recommend examining associations between microclimates and coarser climate variables in both space and time to

	(Lawson *et al.*, 2014; Suggitt *et al.*, 2018). For instance, such an effect might arise in butterfly phenology if individuals experiencing a colder environment seek out warmer microclimates, whilst those in a warmer environment seek out cooler microclimates (Roy *et al.*, 2015).	determine when this will be an issue. See also, recommendation a.i.3.
b) Transferability Issues relating to the transferability of spatial associations over time	**i) Lack of temporal validation** Models are often projected over time, under future (or past) climates, but their ability to accurately predict changes to a system over time is rarely assessed, due to a lack of testing data. Instead, it is commonly assumed that spatial associations capture the temporal response over the timescale of interest.	1) Where opportunities to test the accuracy and precision of equilibrium predictions on appropriate timescales can be identified they should be prioritised. 2) In some instances historic data exist that have been underutilised for hindcasting, e.g., museum and herbarium specimens (Guerin *et al.*, 2012), dendrochronology (Klesse *et al.*, 2020), genomic data (Miller *et al.*, 2021), paleodata (Blois *et al.*, 2013).

		3) Where the timescale of the equilibrium response precludes quantitative analysis, there may be potential to make qualitative predictions over shorter timescales (e.g., 10 years) that are then tested. 4) Where suitable testing data are not available, there is still great value of using simulations to detect limits to inference (Qiao *et al.*, 2019). 5) Space-time comparison provides an opportunity to test whether climate-biotic relationships are of similar magnitude (Table 1aii).
	ii) Assumption of contemporary spatial equilibrium	1) Rather than using a single historical average for each predictor at a site we suggest analysis of a moving window

	A common assumption is that current spatial patterns reflect the equilibrium outcome of eco-evolutionary responses to spatial variation in the long-term average climate. However, there may be a lag between the contemporary biotic response and the equilibrium response (Fig. 2b); whether current spatial patterns are at equilibrium with the climate is unclear, variable across systems (Gaüzère *et al.*, 2018), and largely untested. Recent anthropogenic shifts in climate may have perturbed many systems from their long-term equilibrium. There is potential for the relationship between a climate variable and biotic response to be out of equilibrium in the intercept and/or slope of the response curve and the consequences of either for SFTS predictions are unknown (Coulson, 2021).	of historical climate to identify the time period over which climate best predicts the system. The situation where current biotic states are better predicted by historic rather than current climate may indicate that the system exhibits biotic lag behind the equilibrium. 2) We are not aware of an approach to test whether *in situ* biotic systems are at equilibrium with climate in the absence of temporal data. Therefore, we suggest that theory represents the most promising avenue for exploring the problems that non-equilibrium in intercept and/or slope presents to SFTS methods. 3) If current spatial patterns are not at equilibrium, future projections will indicate transient rather than equilibrium biotic responses. Moving beyond static snapshot

	If a system is in a transient state, and not at equilibrium, this need not invalidate future projections, as these may also be interpreted as indicating the expected transient, rather than equilibrium, response. Equilibrium also does not necessarily imply the system is at its optimum, e.g., phenotypes may be perturbed from their local optima by migration-load, and instead be at selection-migration equilibrium (Hadfield, 2016).	projections to understand how the transient response is expected to change dynamically over fine temporal resolutions (i.e. annual) would provide an indication of (i) the sensitivity of the projected biotic responses to the choice of future time horizon (Petchey *et al.*, 2015) and (ii) the rate, timing and abruptness of the expected biotic response, not just the magnitude.
	iii) Rate of change and response Relationships observed over space are likely to be the result of both long-term and short-term processes, but the immediate temporal responses that are more relevant to climate change predictions (i.e. over decades) will be driven by short-term processes alone (Adler *et al.*, 2020; Münzbergová *et al.*, 2021). Therefore, there may be a lag in the temporal response, with equilibrium not reached in the	A method for quantifying the projected timescale for a lag to be closed and equilibrium reached would be invaluable for predicting consequences. We are not aware of such tools, but suggest that simulation would provide a potential avenue.

	short-term or potentially not reached at all (Chevin, Lande & Mace, 2010). This lag may be exacerbated by future climate change occurring at a faster rate than that in the past, with biotic responses unable to occur rapidly enough to reach equilibrium. Consequently, the timescale over which space-for-time predictions are valid is uncertain.	
	iv) Non-analogue climates In the future, organisms may be exposed to climatic conditions not experienced today, but models do not contain any information about ecological responses to these novel conditions and so rely on extrapolation (Fitzpatrick & Hargrove, 2009). This includes both new values of individual variables but also novel combinations of variable values. This will be a particular issue where linear models are used for non-linear responses. Tipping points may be reached.	1) Where possible, experiments can provide insights into organisms' responses to novel conditions. 2) Similarity between current and future climates can be quantified to assess the level of uncertainty in extrapolation (Qiao *et al.*, 2019). 3) Whilst linear assumptions in modelling are convenient, we encourage wider testing of their adequacy (Iler *et al.*, 2013).