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 an urgent challenge. Since we seldom have sufficient long-term biological data to use the past to anticipate the future, spatial climate-biotic relationships 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 largely developing methods in isolation. We review how climate-focussed SFTS are used in four subfields of ecology and evolution, each focussed on a different type of biotic variable – population phenotypes, population genotypes, species' distributions, and ecological communities. We then examine the similarities and differences between subfields in terms of methods, limitations and opportunities. While SFTS are used for a wide range of applications, two main approaches are applied across the four subfields: spatial *in situ* gradient methods and transplant experiments. We find that SFTS methods share common limitations relating to (i) the *causality* of identified spatial climate-biotic relationships and (ii) the *transferability* of these relationships, i.e. whether climate-biotic relationships observed over space are equivalent to those occurring over time. Moreover, despite widespread application of SFTS in climate change research, key assumptions remain largely untested. We highlight opportunities to enhance the robustness of SFTS by addressing key assumptions and limitations, with a particular emphasis on where approaches could be shared between the four subfields.

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

Contents

I. Introduction

Environmental conditions that vary over space and time can drive changes in biotic variables through processes such as plasticity, adaptation, colonisation and extinction (Parmesan, 2006). For example, climate variables such as temperature and precipitation have impacts on biotic variables ranging from changes in population phenotypes (Bergmann, 1848; Darwin, 1859) and genotypes (Bradshaw & Holzapfel, 2001), to shifts in species' distributions (Merriam, 1894; Grinnell, 1914) and the composition and functioning of ecological communities (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, IPCC 2022). Consequently, there is an urgent call for ecologists and evolutionary biologists to understand and predict how populations, species and ecological communities respond to changes in climate variables.

Given that ecological and evolutionary processes operate over time, predicting the biotic responses (VII. Glossary) to future climate change would ideally use long-term monitoring data to directly observe temporal climate-biotic relationships (VII. Glossary) and project these into the future (time-for-time approach; Figure 1a; Roy *et al.*, 2001; Simmonds *et al.*, 2020). However, long-term ecological data are rare (Estes *et al.*, 2018; Lindenmayer, 2018), as highlighted by recent efforts to collate time-series data (e.g. Dornelas *et al.*, 2018; Comte *et al.*, 2021; Johnson *et al.*, 2022a). The urgent need to make predictions of biotic responses to future climate change has led global change biologists to consider an alternative approach, space-for-time-substitution (SFTS; Figure 1b; VII. Glossary). SFTS use spatial climate-biotic relationships to predict biotic responses to climate change over time, under the assumption of space-time equivalence (VII. Glossary; Table 1; Pickett, 1989). This approach can generate predictions rapidly (e.g. Blüthgen *et al.*, 2022), often from existing data or relatively small datasets that can be produced during single grants. Given this relative feasibility of SFTS compared to time-for-time approaches, SFTS has become near ubiquitous for understanding and predicting biotic responses to climate change (Table 2).

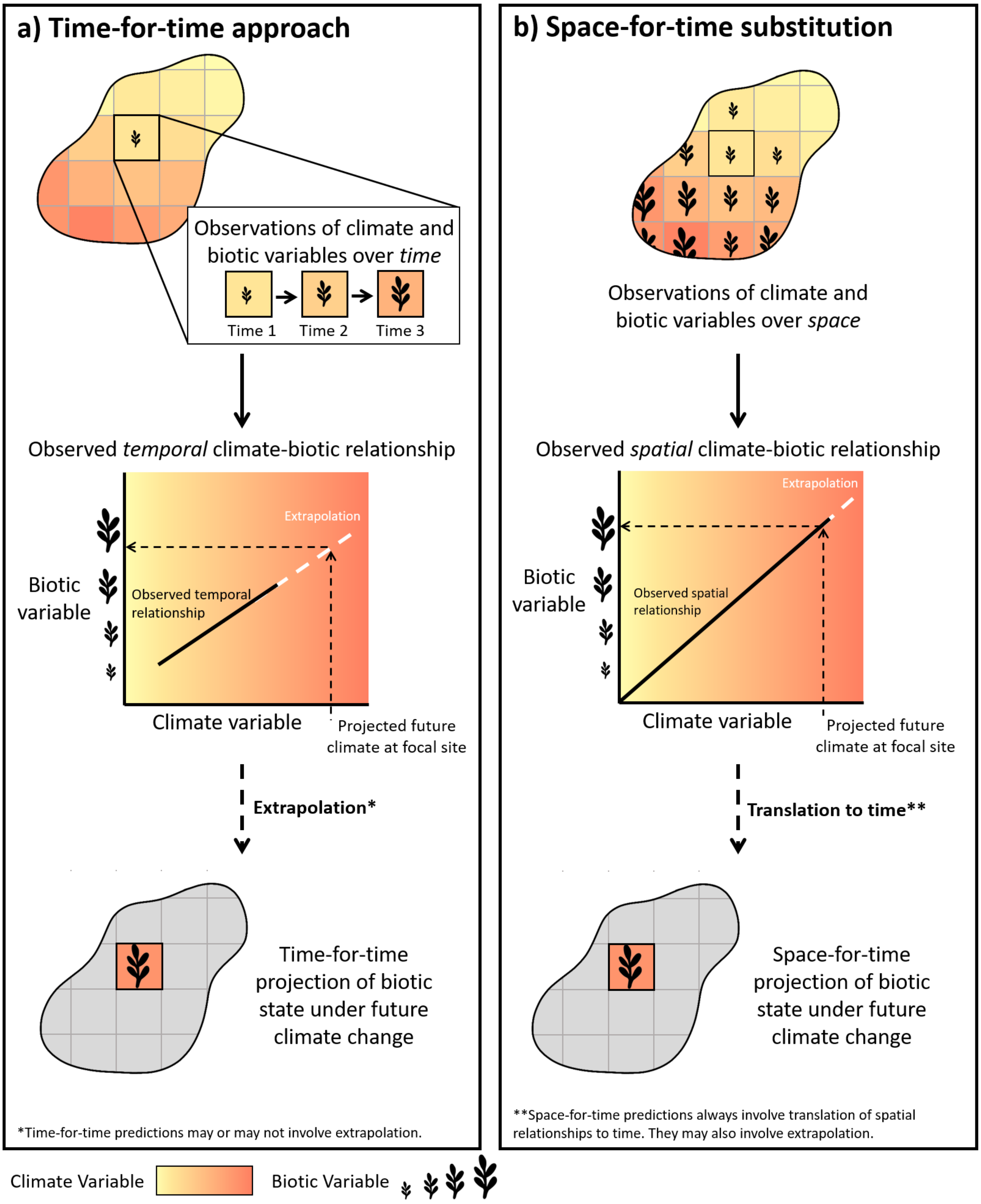

Figure 1: *Approaches for projecting biotic responses to future climate change at a focal site (black square). a) Time-for-time approaches, where climate-biotic relationships are observed over time and extrapolated under projected future climates. b) Space-for-time substitution*

(SFTS), where climate-biotic relationships observed in geographical space are translated to time under projected future climates. Note that time-for-time and space-for-time climate-biotic relationships are not necessarily equivalent.

Studies employing 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, with each gradient type providing different strengths and weaknesses (Verheyen, Tüzün & Stoks, 2019). While the comparative straightforwardness of collecting data for SFTS is an attraction, the method has inherent limitations (Table 3) that need to be acknowledged, explored, and minimized to maximise the robustness of predictions. Namely, for all biotic variables, SFTS relies on the fundamental, often implicit, and rarely tested assumption that climate-biotic relationships observed in space are predictive of those that occur over time (e.g. Phillimore *et al.*, 2010; Isaac *et al.*, 2011; Blois *et al.* 2013).

The use of SFTS in global change research has progressed somewhat independently across subfields focussing on different biotic variables. This review aims to synthesise the use of SFTS across four broad classes of biotic variables: population phenotypes, population genotypes, species' distributions and ecological communities (Table 2). We first describe the most widely used SFTS approaches that are applied across different biotic variables, and highlight limitations that are common to all of our focal 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. For each subfield, we highlight an exemplar SFTS study in Table 2. Third, we discuss the broad challenge of SFTS validation.

Finally, we identify opportunities for improving the robustness of SFTS, including cross-fertilisation of ideas between the different subfields. While the focus of this review is on the use of SFTS to understand and predict the effects of climate variables, many of the insights into methods, assumptions, limitations and validation apply to SFTS across other types of ecological and environmental gradients (e.g. land use intensity, Purvis et al., 2018; ecological succession, Johnson & Miyanishi, 2008).

II. Commonalities of SFTS approaches

There are two main method types that are employed across the four subfields to investigate biotic responses to climate variation over space: *in situ* gradient approaches (VII. Glossary) and transplant experiments (VII. Glossary). These are compared in Figure 2 and Table 1. *In situ* gradient methods involve observing the value of a biotic variable, hereafter 'biotic states' (VII. Glossary), at multiple sites along a spatial climate gradient to allow estimation of the spatial climate-biotic relationship (Figure 2a, Table 1a; Dunne *et al.*, 2004). Note that *in situ* gradients could also refer to observed temporal gradients, but we use the term for spatial gradients only. A variant of the *in situ* gradient approach that was developed for studying species distributions is ecological niche models (ENMs; 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). The *in situ* gradient method presents a comparatively low logistical hurdle to data collection, meaning that spatial replication (i.e. number of sampling locations) is often high (e.g. Morán-Ordóñez *et al.*, 2017). However, a correlative *in situ* gradient approach in isolation is typically uninformative about the processes that generate the spatial pattern of a biotic state, such as the relative contributions of short-term processes including phenotypic plasticity (VII. Glossary) versus longer-term equilibrium (VII. Glossary) processes such as local adaptation (VII. Glossary; Table 1a; Adler, White & Cortez, 2020).

The second main SFTS approach involves transplant experiments, either as (i) a common garden transplant (VII. Glossary) to a shared environment, including experimentally manipulated environments (Figure 2b; Table 1bi), or (ii) a reciprocal transplant (VII. Glossary) between pairs of sites (Figure 2c, Table 1bii). Transplant experiments can yield information on the processes (e.g., plasticity versus genetic divergence) that generate spatial climate-biotic relationships (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.*, 2022b), which makes it difficult to identify the causal driver(s) of biotic responses. There are also many taxa for which transplant experiments are challenging or unfeasible, and most transplant experiment have involved organisms that are more easily moved, such as plants (e.g., Alexander, Diez & Levine, 2015).

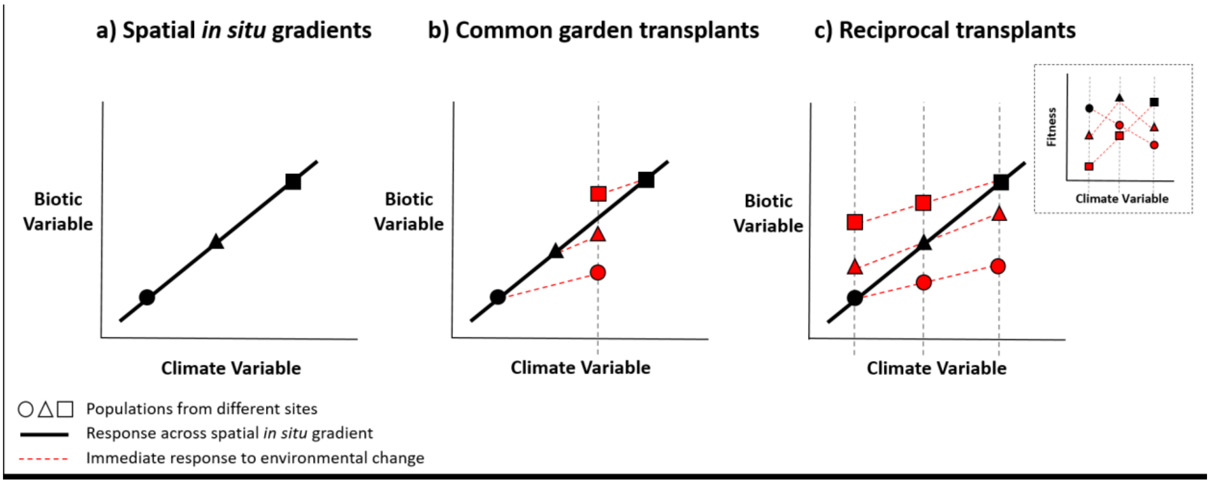

Figure 2: *The main methods used to identify spatial climate-biotic relationships for SFTS: (a) spatial in situ gradients and (b,c) transplant experiments. Across all plots, shapes represent populations that have different sites of origin. (a) in situ gradient approaches, where biotic states observed at sites across a spatial climate gradient are used to model climate-biotic relationships (black line). (b,c) transplant approaches where organisms are moved across space into different environments. Here, dashed red lines indicate an immediate biotic*

response to a new environment (e.g. phenotypic plasticity). Transplant approaches are (b) common garden transplants, 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 case when the biotic variable is fitness and each population is the fittest at its site of origin (indicating local adaptation; Kawecki & Ebert, 2004*). Note that while linear climate-biotic relationships are depicted, non-linear relationships are possible.*

Two extensions of the SFTS approach have been developed to predict the vulnerability (VII. Glossary) of biodiversity to climate change; we term these metrics 'biotic offsets' and 'biotic lags' (Figure 3). The first, a biotic offset (VII. Glossary; Figure 3a), is defined as the difference between the observed biotic state at a site and the predicted equilibrium biotic state at that site under a future climate (Fitzpatrick & Keller, 2015; Frank *et al.*, 2017). This type of metric has also been termed vulnerability (Bay *et al.*, 2018), risk of nonadaptedness (Rellstab *et al.*, 2016), and (relative) risk of maladaptation (St Clair & Howe, 2007). Here we use the term biotic offset – inspired by the 'genetic offset' introduced by Fitzpatrick and Keller (2015) – to apply to any biotic variable. The second metric, a biotic lag (VII. Glossary; Figure 3b), is the difference between the observed biotic state at a site and the predicted equilibrium biotic state at that site under the current climate conditions. This has been variously termed maladaptation (e.g. Hällfors *et al.*, 2020), disequilibrium (e.g. Sandel, 2019) and climatic debt (e.g. Devictor *et al.*, 2012). In some studies, the biotic lag is translated into a spatial distance (Devictor *et al.*, 2012). This involves quantifying the shift in (i) a biotic state and (ii) climate over a given time period, and identifying the geographic distance over which a shift of the same magnitude can be observed (Balanyá *et al.*, 2006). The extent to which the geographic distance for climate exceeds that of the biotic state is the 'distance of biotic lag' (VII. Glossary; Figure 3c; Table1aiii; Devictor *et al.*, 2008, 2012; Ash, Givnish & Waller, 2017). For example, Devictor *et al.* (2012) examined temporal and spatial trends in temperature and community temperature indices (CTI – a measure of the thermal ranges of the species in a community) for birds and butterflies across Europe. They found that the increases in temperature that had been observed over 18 years corresponded to a northwards shift of 249 km, whilst the equivalent shifts in CTI for birds and butterflies was 37 km and 114 km, respectively, corresponding to biotic lag distance of 212 km and 135 km.

Common to most ecological and evolutionary applications of SFTS is the often implicit expectation that spatial climate-biotic relationships will arise via a combination of comparatively rapid processes and slow processes, and may potentially be at equilibrium (Dunne et al. 2004; Adler *et al.* 2020). For instance, phenotypic plasticity is a rapid process, whereas genetic adaptation and shifts in species distributions are slower processes that generally take place over multiple generations. Conversely, in the short-term, temporal climate-biotic relationships will often be dominated by rapid processes, and it may only be over longer time-scales that slower acting processes will come to the fore (Dunne et al. 2004; Adler *et al.* 2020).

Whilst SFTS offers substantial promise as a tractable approach for generating much needed biotic predictions (Fukami & Wardle, 2005), several general limitations exist that, in the absence of successful validation, may undermine the robustness of SFTS projections. Limitations fall into two broad categories, causality and transferability. These are discussed in detail in Table 3 (note that this is a non-exhaustive list), and so here we give only a brief overview of the issues. The first type of limitation, causality, relates to the fact that correlative methods may fail to capture the true causal effect of a climate variable on a biotic variable (Table 3a). This can arise from suboptimal selection of focal climate predictors, inadequate sampling, spatial autocorrelation, and the spatial scale of variables used (see Table 3a for details). The second type of limitation, transferability, relates to the fact that robust projection of future biotic changes relies on the assumption that climate-biotic relationships are equivalent in space and time, and that these relationships will hold under future climates (Table 3b; Blois *et al.*, 2013; Sequeira *et al.*, 2018; Yates *et al.*, 2018). Limitations relating to transferability include lack of validation over time (space-time equivalence validation, see section IV), the largely untested assumption of contemporary spatial equilibrium, rates of change in climate and biotic variables, and the occurrence of novel future climates (see Table 3b for details). Alongside a discussion of the limitations, Table 3 includes recommendations and improvements to address these issues and thus improve the robustness of SFTS.

III. Application of SFTS to climate-biotic relationships

(1) Population phenotypes

Correlations between spatial climate gradients and population phenotypes have long been observed, including a tendency for body mass to decrease with increasing temperatures (Bergmann, 1848) and spring phenology to advance with increasing temperatures (Hopkins, 1919). SFTS informed by *in situ* gradients and transplant experiments have been 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, 2022), 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 in isolation to generate a space-for-time prediction for phenotypic data, the spatial phenotypic response is sometimes implicitly assumed to be entirely driven by phenotypic plasticity, such that the response will be immediate (Jaramillo *et al.*, 2017), or the underlying mechanism and timescale of predictions are vague. Where phenotypic and climate data are available in time as well as space, the spatial climate-phenotype relationship can be compared to that over time and this may provide insight into the processes that contribute to the spatial climate-phenotype relationship. When making such space-time comparisons (VII. Glossary), the temporal slope of a climate-phenotype relationship estimated over years to decades is assumed to arise primarily due to plasticity, whereas the spatial slope is assumed to arise from plasticity plus local adaptation (VII. Glossary; Phillimore et al. 2010). Space-time comparisons using phenology and temperature data have been used to draw inferences about (i) the contributions that climate-mediated phenotypic plasticity and local adaptation make to the spatial climate-phenotype relationship (Phillimore *et al.*, 2010; Hodgson *et al.*, 2011; Roy *et al.*, 2015; Delgado *et al.*, 2020) and (ii) biotic lags and offsets (Figure 3) (Phillimore *et al.*, 2010). As far as we are aware, most space-time comparisons have used phenological data (but see Youngflesh *et al*. 2022 for an example using morphological data), reflecting the abundance of extensive spatiotemporal phenological data arising from citizen science schemes.

Where the goal is to separate the contributions that phenotypic plasticity and genetic divergence (including local adaptation) make to spatial variation in phenotypes, transplant experiments have a long history (Turesson, 1922). The contribution of phenotypic plasticity can be quantified as the difference in phenotypes between environments when holding the genotype constant (Stamp & Hadfield, 2020). Whereas the contribution of genetic differentiation can be quantified as the difference between population phenotypes when holding the environment constant in a shared common garden. The ‘gold-standard’ for identifying local adaptation involves comparing fitness (a special case of a phenotype) of populations following a reciprocal transplant (Savolainen, Lascoux & Merilä, 2013). Here, local adaptation is inferred where both (i) populations are fitter in home than away environments, and (ii) local populations are fitter than foreign populations (Kawecki & Ebert, 2004; Blanquart *et al.*, 2013). A challenge with all these approaches is to establish a causal role of climate variables, with replication across populations and/or sites often insufficient for this purpose (see Table 1b and 3a).

Transplant experiments that succeed in identifying the processes underpinning spatial climate-phenotype relationships, can then inform as to the nature and timescale of the phenotypic response to climate change. For instance, where a plastic response to a climate variable is identified, phenotypic responses to climate change are expected to be immediate, as found, for example, in the reproductive phenology of grassland plants (Frei *et al.*, 2014) and foliar traits in beech and spruce saplings (Sanginés de Cárcer *et al.*, 2017). 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). Transplant studies can also be used to infer whether phenotypic responses are lagging behind changing climate conditions (Figure 3b). For example, Wilczek et al. (2014) found that when populations of *Arbaidopsis thaliana* were transplanted to four regions of Europe, local populations were generally fitter than foreign populations. However, the most northerly population was less fit than a more southerly population, which the authors interpreted as evidence that adaptation of the northern population was lagging behind the optimum as the climate warmed (see table 2a for further discussion).

Transplant studies can also be used to calculate the phenotypic offset (Figure 3a) of populations to future climates (often termed ‘relative risk of maladaptation’) (St Clair & Howe, 2007; Frank *et al.*, 2017; Rellstab, Dauphin & Exposito-Alonso, 2021). The phenotypic offset approach was originally developed to identify the best seeds to plant in different spatial locations, based on the climatic differences between the planting site and the seeds' site of origin (Campbell, 1986). This approach combines common garden estimates of phenotypic distributions within populations, phenotypic differences between populations, and *in situ* information on how mean phenotypes change with climate. However, to date the phenotypic offset approach has not been widely applied (Frank *et al.*, 2017).

The major limitations that are most pertinent to phenotypic SFTS are limited to those that apply broadly across biotic responses (Table 3), though the nature of these limitations can be quite different depending on whether an *in situ* gradient or transplant approach has been adopted.

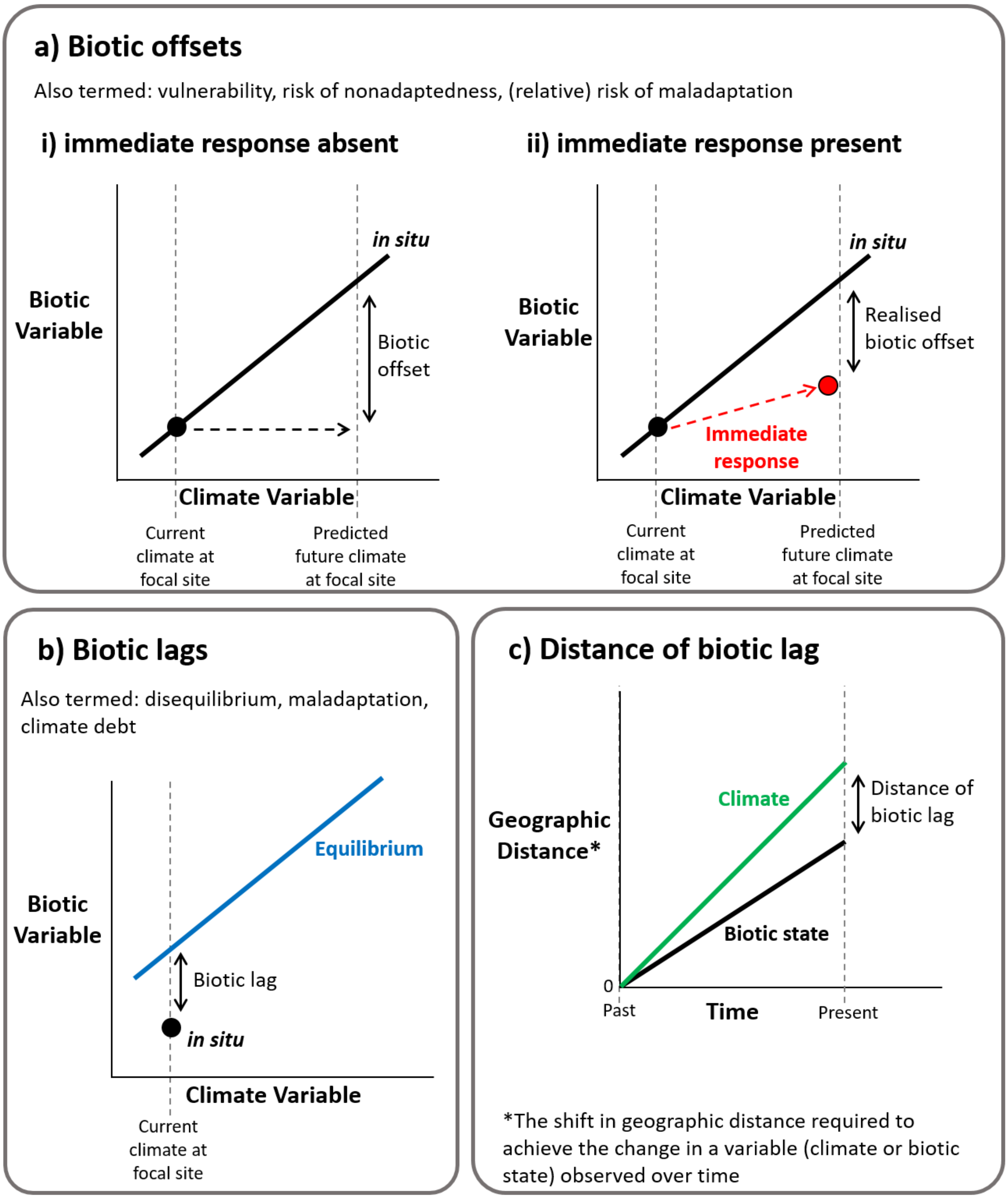

Figure 3: *Metrics of the vulnerability of biodiversity to climate change based on SFTS. Black circles represent a focal site. (a) biotic offsets, the distance between the current biotic state at a focal site and the predicted equilibrium biotic state at that site under future climate conditions. The current biotic state may either be (i) that observed in situ at the focal site or (ii) that accounting for an immediate biotic response to climate change (e.g. due to*

phenotypic plasticity; red circle), which can be observed via a transplant experiment 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 biotic 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 climate-biotic relationships are depicted here for simplicity but some relationships may be non-linear. Note that where the biotic response is a species' distribution, the focus is generally on how the biotic state (presence or abundance) covaries with climate across many populations, rather than a single population as depicted here. Where the biotic response is species' occurrence, the biotic state can be thought of as either the probability of presence or the climate suitability.

(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 small proportion making explicit predictions regarding the impact of climate change on genotypes (e.g. Row *et al.*, 2014; Jordan *et al.*, 2017; Martins *et al.*, 2018; Exposito-Alonso *et al.*, 2018). Transplant studies are also used to study genetic markers, with the motivation usually to identify the genetic loci underlying climate-phenotype relationships, rather than direct correlations between genotypes and climate (Fournier-Level *et al.*, 2011; de Villemereuil *et al.*, 2018; Housset *et al.*, 2018). Although, where the focus of transplant studies is on fitness-associated genotypes, it is possible to estimate climate-genotype relationships (Fournier-Level *et al.*, 2011) and make predictions about how allele frequencies will respond to future climate change (Exposito-Alonso *et al.*, 2018, 2019)**.**

Two methods are commonly applied across *in situ* gradients to identify climate-genotype relationships and the putatively adaptive loci (VII. Glossary) (Schoville *et al.*, 2012; Hoban *et al.*, 2016; Li *et al.*, 2017). The first is genotype-environment association analysis, which estimates climate-genotype relationships across a climate gradient (Rellstab *et al.*, 2015). The second, differentiation outlier methods, involves identification of the loci that are most highly differentiated between different climates and therefore most likely to be involved in local adaptation (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). The focal genotypes can be specific candidate genes, known or suspected to be associated with a particular function that may be involved in a genetic response to climate, such as the relationship between latitude (as a proxy for climate) and alcohol dehydrogenase polymorphism in *Drosophila melanagoster* (Umina et al., 2005). Alternatively, multiple regions of the genome can be screened to identify the molecular markers (often single nucleotide polymorphisms, SNPs) exhibiting the strongest relationships with climate variables (Hancock *et al.*, 2011; Bay *et al.*, 2018). This was the approach adopted in a study of yellow warblers in the US, which found that of over 100,000 SNPs, approximately 200 were highly correlated with spatial variation in precipitation (Bay et al. 2018, see table 2b for further discussion).

Climate-genotype relationships identified across *in situ* gradients can be used to make SFTS predictions 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 – first developed for studying species' distributions (Pearson & Dawson, 2003;

Guisan & Thuiller, 2005; Elith & Leathwick, 2009) – have been applied to identify climate-genotype relationships from *in situ* gradients (Jay *et al.*, 2012; Fitzpatrick & Keller, 2015) or common garden transplants (Exposito-Alonso *et al.*, 2018, 2019) and used to predict changes in the distribution of alleles or selection pressures under future climates. Analogues of ecological niche models (section III(3)) 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)). SFTS predictions are increasingly being used to find the biotic (genomic) offset (Figure 3ai) (Fitzpatrick & Keller, 2015), the difference between current genetic compositions and those projected to be required under climate change. This 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 (Fitzpatrick & Keller, 2015). The genomic offset is variously termed genetic offset, genomic vulnerability, and risk of nonadaptedness (reviewed by (Capblancq *et al.*, 2020; Rellstab *et al.*, 2021; Hoffmann, Weeks & Sgrò, 2021).

There are two main types of limitations that are particular to genotypic SFTS. The first is in identifying the causal loci underlying adaptation to climate. Multi-marker screening methods for identifying adaptive loci are prone to false positives (Hoban *et al.*, 2016); neutral alleles may appear to exhibit variation with a climate 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 (Rellstab *et al.*, 2015, 2021; Hoban *et al.*, 2016; Li *et al.*, 2017; Booker, Yeaman & Whitlock, 2021; Hoffmann *et al.*, 2021). In addition to false-positives, multi-marker screening methods are also prone to false negatives. This can arise because local adaptation often results from small changes at many loci (i.e. it is polygenic), and a single phenotype may be achieved through multiple different combinations of genotypes across loci (i.e. redundancy; Yeaman, 2015; Hoffmann *et al.*, 2021). This results in low power to detect each locus' effect (Hoban *et al.*, 2016; Rellstab *et al.*, 2017; De La Torre, Wilhite & Neale, 2019; Hoffmann *et al.*, 2021). However, although high redundancy hinders prediction of the genomic response to environmental change, it is usually associated with greater adaptive potential, resulting in better predictability of *phenotypic* responses for polygenic traits compared to those controlled by a small number of loci (Kardos and Luikart 2021). The second limitation of genotypic SFTS is that the critical assumptions required for this approach to work may often not be met because the loci involved in adaptation in space and time may differ. For example, adaptation in time may occur via the emergence of novel genotypes (Booker, Yeaman & Whitlock, 2021), whereas the presence of maladaptive gene flow or a lack of adaptive gene flow can hinder adaptation in time (Lenormand, 2002). As a result, even with perfect knowledge of the complete set of loci involved in adaptation to climate in space, we may fail to predict genotypic change over time.

(3) Species distributions

The most prolific use of space-for-time substitutions in climate change ecology and evolution is in using ecological niche models (ENMs; Table 1a) to predict climate risks to populations or how species' distributions will shift as the climate changes (Elith & Leathwick, 2009; Melo-Merino, Reyes-Bonilla & Lira-Noriega, 2020). In the SFTS context, ENMs estimate the spatial relationships between multiple climate variables and a species' geographical distribution (occupancy or abundance) over *in situ* gradients (Pearson & Dawson, 2003; Guisan & Thuiller, 2005; Elith & Leathwick, 2009) and use this to predict species' potential future distributions/risk (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 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. In the context of modelling climate-species relationships, transplant experiments are also used, but at a much lower frequency than *in situ* gradient approaches.

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 are also 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 margins or centroids; Lenoir *et al*., 2020) rather than within a single population (as shown in Figure 3b). 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 (Figure 3b; Lewthwaite *et al.*, 2018; Soultan *et al.*, 2022). Biotic lags can also be quantified in terms of spatial distance (distance of biotic lag; Figure 3c; Ash *et al.*, 2017). Similarly, comparing observed geographical shifts in climate variables and species distributions can indicate the presence of a biotic lag, and can be used to reveal how much of the distributional shift is explained by the shift in climate (Lenoir *et al*., 2020). 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 colonisation rate, which can then be compared to the rate required under future climate change (Brodie *et al.*, 2021).

In comparison with the *in situ* gradient approach, the application of transplant experiments to species-focussed SFTS is much less common. Transplants of individuals to sites either within or beyond a species' current geographical range have been used to provide insights into the factors limiting species' ranges (e.g. climate variables, dispersal limitation, biotic interactions), the presence of biotic lags, and species' responses to future climate change (e.g. Marsico & Hellmann, 2009; Willis *et al.*, 2009; Pelini *et al.*, 2009; Van der Veken *et al.*, 2012). For example, Willis *et al.* (2009) transplanted two UK butterfly species to a site beyond their range margins and used the successful establishment of these populations to infer the presence of a biotic lag.

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), and so we focus on the assumptions made when ENMs are used for SFTS projections of climate change impacts. In particular, there is an assumption that either (i) the realised climatic niche is conserved over time or climate is the sole determinant of species' distributions and (ii) 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) a shift in climate not being accompanied by shifts in the other variables that limit a species' 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 community responses to future climate change. These have focussed on two facets of communities. The first is community composition, which includes species composition (e.g. identity, richness; Nooten, Andrew & Hughes, 2014; Niu *et al.*, 2019; Kinard, Patrick & Carvallo, 2021) and trait (or functional type) composition (Dubuis *et al.*, 2013; de Oliveira *et al.*, 2020). This includes metrics such as the community temperature/precipitation index (CTI/CPI), which captures the climate conditions encountered within the geographic ranges of the species within a community (Devictor *et al.*, 2012). The second is species interactions, including consumer-resource (Rasmann *et al.*, 2014; Tran *et al.*, 2016), competitive (Alexander *et al.*, 2015), symbiotic (Steidinger *et al.*, 2019), and parasite(-vector)-host (Pickles *et al.*, 2013). Where the focus is on species composition and species interactions, community focused SFTS are effectively extensions of species-focussed approaches, and where the focus is on community traits they are extensions of phenotype-focussed SFTS. As a consequence, many of the same methods and limitations are relevant.

In situ gradient methods, often ENMs, 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). Three main approaches are used (Ferrier & Guisan, 2006; Nieto-Lugilde *et al.*, 2018): (i) modelling the relationship between climate and a community-level attribute, such as species grouped into vegetation classes (Hilbert & Ostendorf, 2001; Pearson *et al.*, 2013); (ii) modelling individual species' responses to future climate change and overlaying their potential distributions to make community-level inferences (stacked models; Thuiller *et al.*, 2006; Gallagher, Hughes & Leishman, 2013; Davis, Champion & Coleman, 2022); or (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 a species. Where temporal and spatial data are available, inferences can also be made about the presence of a biotic lag in the temporal community response to climate change (Figure 3b), using analogous approaches as described for phenotypes (space-time comparison; Sandel, 2019; Gaüzère *et al.*, 2020; Section III(1)) or species distributions (comparing observations to predictions from a different time; Menéndez *et al.*, 2006; Bertrand *et al.*, 2011; Section III(3)). These biotic lags can also be quantified in terms of geographic distance (Distance of biotic lag, Figure 3c; Devictor *et al.*, 2008, 2012).

For community trait compositions, SFTS can provide insights into the processes that have generated spatial patterns and thus may be involved in community responses to future climate change (Lajoie & Vellend, 2018). In particular, the relative contributions of interspecific processes (species turnover) and intraspecific processes (plasticity and genetic differentiation; Section III(1)) can be separated. This involves comparing the slopes estimated between a climate variable and (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).

Community focused transplants present considerable logistical challenges, and so their application has been relatively limited. The most straightforward approach involves moving a single species into a new community, 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). More challenging, is to simultaneously move multiple species into new environments to provide insights into how a community may respond to 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). Alexander *et al.*, (2015) combined both of these approaches by transplanting both individual species and a multi-species plant community to different elevations in the Alps to explore the potential impacts of novel interactions and increased temperatures (see Table 2d for details).

Community-focussed SFTS are subject to similar limitations as for species (Section III(3)) and phenotypes (Section III(1)), with additional complexities that arise when considering multiple species together. For example, different species may shift their distributions and phenologies in different ways in response to climate change, resulting in complex changes in community compositions and biotic interactions (Tylianakis *et al*., 2008; Kharouba *et al*., 2018; Beissinger & Riddell, 2021; Roslin *et al*., 2021; Antão *et al*., 2022) that are not captured by contemporary *in situ* gradients and transplant experiments. Alternatively, it is possible that community responses to climate change may be more predictable if the consideration of multiple species averages away some of the stochasticity in individual species' responses (Srivastava *et al*., 2021). Additional limitations arise with multi-species transplants because they tend to involve (i) a sample 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, the issue of inadequate spatial replication is particularly pronounced for community-focused transplant experiments 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, see Table 2b), which precludes robust inference of a causal climatic variable (Table 3a).

IV. Validation of SFTS

Across all four 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. The predictive ability of SFTS appears to vary across different ecological contexts including biotic variables (e.g. Bjorkman *et al.*, 2018), taxa (e.g. Dobrowski *et al.*, 2011) and timescales (e.g. Roberts & Hamann, 2012). A quantitative analysis of the scenarios under which SFTS perform best is a priority for future work in this area. In the interim, we suggest that SFTS may perform better when the level of extrapolation is minimised (e.g. Fitzpatrick *et al.*, 2018a; Sequeira *et al.*, 2018; Qiao *et al.*, 2019) and should be approached with caution where successful validation is lacking for a study’s specific system and context.

Two types of validation are needed when a SFTS projection is made. First, we need to test whether the climate variable(s) is/are causal of the biotic variation observed through space, which we term ‘spatial validation’ (Table 3a). Opportunities for spatial validation include non-independent spatial data (e.g. data splitting; Berry *et al.*, 2002; Norberg *et al.*, 2019), independent spatial data from a different location (i.e. replication; e.g. Randin *et al.*, 2006;

Early & Sax, 2014) or experiments (including transplants; Hancock *et al.*, 2011). Where there has been successful spatial validation, this increases our confidence that the identified drivers are causal, but it does not test transferability. The second validation type, which we term ’space-time equivalence validation’, involves comparing spatial climate-biotic relationships with temporal relationships or SFTS projections with temporal data. Assuming that causal relationships have been estimated in space, then the space-time equivalence validation tests the central assumption of space-time transferability (Sequeira *et al.*, 2018; Table 3b). Different types of data can be used for space-time equivalence validation (Rellstab *et al.*, 2021), 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-based inference (Miller *et al.*, 2021), and *in silico* (Qiao *et al.*, 2019).

When conducting space-time equivalence 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 3b; Petchey *et al.*, 2015; Adler *et al.,* 2020). Note that testing for biotic lags (Figure 3b) – which generally involves comparing temporal climate-biotic relationships to those expected based on the spatial relationship – is a type of space-time equivalence validation, where one can assess whether the biotic response is in the correct direction, with additional inferences made about whether the biotic state is lagging behind the equilibrium biotic state.

Ideally, both successful spatial validation and successful space-time equivalence validation should support any application 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 where further validation is needed.

Population phenotypes: Neither spatial nor space-time equivalence validation is common practice when analysing correlative climate-phenotype relationships across *in situ* gradients or transplant experiments. This 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 variables. There are a handful of instances of space-time equivalence validation using historical data (Hodgson *et al.*, 2011; Guerin *et al.*, 2012; Jochner, Caffarra & Menzel, 2013) and repeated experiments (Bradshaw & Holzapfel, 2001). Additionally, space-time comparisons have also been used to assess the extent to which spatial climate-biotic relationships are transferable over time (Table 1aii; Phillimore *et al.*, 2010, 2012; Kharouba *et al.*, 2014; Klesse *et al.*, 2020; Wu *et al.*, 2022).

Population genotypes: Where validation has been conducted at the genotypic level, it has typically focussed on spatial validation rather than space-time equivalence validation. Spatial validation is often assessed by using multiple approaches to identify putatively adaptive loci – both genome-environment association analyses 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). Indeed, there are cases where a locus shows parallel adaptation to climate in different regions (Umina *et al.*, 2005; van Boheemen & Hodgins, 2020). 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 (Barrett, Rogers & Schluter, 2008; 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's climate (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 relationships 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 dearth of suitable long-term genetic data. Indirect space-time equivalence validation of genomic offset predictions can be made by comparison with data on population trends from surveys (Bay *et al.*, 2018, but see Fitzpatrick *et al.,* 2018a, Table 2b), or by measuring proxies for fitness in the wild (Borrell *et al.*, 2020).

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), transplants (Willis *et al.*, 2009; Dixon & Busch, 2017; Merlin, Duputié & Chuine, 2018; Greiser *et al.*, 2020) or simulations (Beale, Lennon & Gimona, 2008), but most often validation is conducted using non-independent data which can lead to severe underestimates of parameter uncertainty (Araújo *et al.*, 2005; Bahn & McGill, 2013; Santini *et al.*, 2021). Introductions of alien species provide an opportunity for spatial validation of the relationships estimated by an ENM. For instance, in a study of plant species that were native to Europe and invasive in North America, Early and Sax (2014) found that

ENMs calibrated on the native range had mixed performance in terms of predicting occupancy in North America, with performance improving for species with larger native geographic extents.

Underlying an ENM prediction of a species' geographic distribution is a description of its niche in terms of a climate-species relationship for each climate variable and rankings of the importance of each variable can be obtained; 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 dominant climate variables (Buermann *et al.*, 2008; Convertino *et al.*, 2012) or (ii) comparing climate-species relationships and/or climate 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 relationships 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).

Space-time equivalence validation of ENMs has used historic data including past species distribution records (e.g. Araújo *et al.*, 2005;; Dobrowski *et al.*, 2011; Rapacciuolo *et al.*, 2012; Brun *et al.*, 2016; Morán-Ordóñez *et al.*, 2017), paleodata (e.g. Pearman *et al.*, 2008; Veloz *et al.*, 2012), simulations (Qiao *et al.*, 2019; Santini *et al.* 2021), comparisons of predictions made using spatial data and time series data (Isaac *et al.*, 2011) and space-time comparisons (Oedekoven *et al.*, 2017; Bradter *et al.*, 2022).

Ecological communities: Spatial validation of community-focussed SFTS often involves non-independent data, such as with data partitioning (Norberg *et al.*, 2019; Zurell *et al.*, 2020), and sometimes utilises spatially independent data (Loewen, Jackson & Gilbert, 2023). 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-phenotype 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.

Space-time equivalence validation of community responses has been assessed using historical data including observations in the recent past (e.g. Lemoine, Schaefer & Böhning-Gaese, 2007; Algar *et al.*, 2009; Kharouba, Algar & Kerr, 2009; Bjorkman *et al.*, 2018) and paleodata (Blois *et al.*, 2013; Maguire *et al.*, 2016). Another space-time equivalence validation approach 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).

Feasibility and logistics of SFTS validation: Both spatial and space-time equivalence validation are essential for ensuring the accuracy of projections, yet validation is strikingly scarce. In some cases, such as space-time equivalence validation for species distributions, validation is 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 (space-time equivalence validation). Given that successful validation is essential for generating robust predictions, a greater value should be placed on this component of SFTS.

V. Opportunities for SFTS

The acute challenge of predicting the biotic impacts of rapid anthropogenic climate change (IPCC 2022) means that SFTS is likely to remain a convenient and vital tool. Here, we consider some of the major ways in which robustness of predictions could be improved, with an emphasis on how approaches could be transferred among the four subfields; see Table 3 for a more comprehensive overview of how the major limitations of SFTS may be addressed.

The challenge of identifying causal climate-biotic relationships is common to all SFTS (Table 3a), but is most acute for transplant studies. Many transplant studies consider just a single transplant site and few source populations (Johnson *et al.*, 2022b) and are thus lacking power to detect a causal climate-biotic relationship. One remedy is to encourage greater replication across sites, climate gradients and gradient types (e.g. altitudinal and latitudinal) to a level that provides adequate statistical power. We recognise that increasing replication will incur substantial logistical and financial costs, but this is essential to establish causality before making SFTS predictions.

A related issue is in giving appropriate attention to the selection of putatively causal climate variables (Table 3ai), and there are approaches used in some of the assessed 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 simultaneously and nonlinear climate-biotic relationships. On the other hand, some phenotype-focused studies aim to narrow down the seasonal period over which a climate variable is important (Simmonds, Cole & Sheldon, 2019) using approaches such as slidingwindows (see van de Pol *et al.*, 2016) and penalised signal regression (see Roberts, 2008). These methods could usefully be applied by other eco-evolutionary subfields to give more focus to the specific climate variables used, the timing over which they are important for driving biotic responses, and the type of relationship with the biotic variable (e.g. quadratic) (Table 3ai).

The other major challenge across SFTS relates to the temporal transferability of spatial climate-biotic relationships (Table 3b). An underutilised avenue for space-time equivalence validation lies with historical data: SFTS 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 (Zurell *et al.*, 2010; Qiao *et al.*, 2019). Powerful methods for simulating realistic genome evolution now make this particularly feasible for testing inference at the genomic level (Haller & Messer, 2019; Láruson *et al.*, 2022). Furthermore, while many studies project biotic responses to climate change at 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 biotic responses and so may overestimate long-term predictability. Finally, as well as validating SFTS predictions for a single point in time, comparison of the slopes (i.e. direction and magnitude) of spatial and temporal climate-biotic relationships (space-time comparison; Phillimore *et al.* 2010; Table 1aii) as we describe for population and community phenotype data could be applied more widely. This represents an opportunity for space-time equivalence 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.

Many biodiversity projections are based on a static ‘snapshot’ approach, where a SFTS model is projected forwards in a single step using climatic conditions averaged over some future, often remote, time period (e.g. Thomas *et al.* 2004; Table 2c). As a result, an important aspect of temporal transferability of SFTS (Table 3b) relates to whether current biotic states are at equilibrium with the environment (Gaüzère *et al.*, 2018) and to the timescale of projection (Adler *et al.*, 2020). If current climate-biotic relationships are at equilibrium, then SFTS based snapshot projections will indicate the future biotic state(s) expected at equilibrium. In contrast, if current climate-biotic relationships are not at equilibrium and lag behind recent climate change, then future snapshot projections will underestimate the magnitude of the biotic response. However, such underestimation does not necessarily invalidate SFTS projections as they may still reliably indicate the direction and magnitude of the *transient* biotic response. Specifically, if the biotic lag is constant over time (i.e. the biotic state remains a consistent distance from the equilibrium biotic state), then projections would still be expected to reliably indicate the magnitude of the transient biotic response (Blonder *et al*. 2017). On the other hand, if the biotic lag is growing over time, due for instance to accelerating climate change, or more complex response dynamics (Blonder *et al*. 2017), then projections would underestimate the magnitude of the transient biotic response.

An important avenue for research is to quantify biotic lags and how these may be expected to change over time. For example, ENMs typically use historical averages of climate variables (e.g. 30 year averages from WorldClim; Fick & Hijmans, 2017), but a sliding window approach (van de Pol *et al.*, 2016) could be applied to identify the decadal period over which historical climates best predict the current biotic state, which may provide an opportunity to identify biotic lags. Similarly, when making projections of future biotic responses to climate change, fine temporal resolution climate data (e.g. daily to annual) 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 biotic responses that is not provided by static snapshot projections (Trisos, Merow & Pigot, 2020).

Another priority for future work on SFTS is to establish the timescale over which future projections are made and how they should be 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 using historical data (e.g. Roberts & Hamann, 2012; Blois *et al.*, 2013; Morán-Ordóñez *et al.*, 2017; Bradter *et al.*, 2022) or *in silico* simulations (Adler *et al.*, 2020). Additionally, dynamic process-based models (e.g. Buckley *et al.,* 2010; Bush *et al*., 2016) offer considerable potential for projecting biotic responses to climate change over time. In such models, rather than making snapshot projections for a single time point, biotic responses are iterated forwards through time, constrained by empirically estimated parameters describing rates of key ecological or evolutionary processes (Morin, Augspurger & Chuine, 2007).

Any assessment of SFTS predictive performance will be sensitive to what 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 (VII. Glossary) 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 (Trisos, Merow & Pigot, 2021). 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 (e.g. Buckley *et al.,* 2010; Bush *et al.,* 2016), or at least dynamic projections of climate change, rather than static snapshots. Genomic studies would also benefit from greater clarity on what we are trying to predict. Unlike ENMs, genotype-environment association analyses are only informative about the *relative* fitness of different genotypes in a given environment. As they do not reveal *absolute* fitness, this means that they cannot tell us whether the population growth rate will become negative in a given environment (Brady *et al.,* 2019).

From examination of the tools used in the four subfields, it is evident that greater communication amongst these subfields could benefit the progression of SFTS methods. In some cases, different subfields have developed equivalent inferential tools independently and this is particularly evident in the case of what we have termed biotic lags and offsets (Figure 3). However, the opportunities to readily identify these parallels may have been reduced by each subfield adopting its own terminology. We hope that that by emphasising the similarities of aims, tools, limitations and challenges across these different eco-evolutionary subfields that this review will foster greater communication and exchange of ideas.

One additional opportunity that applies across all subfields is to broaden spatial and taxonomic representation. Most SFTS studies to date have focused on biotic systems in Europe, North America and Australia, with ENM being the only approach that is widely applied across all continents. Taxonomically, most studies employing transplant methods have involved plants and invertebrates for logistical reasons. Any studies that find ways to broaden the taxonomic scope promise to be highly informative (e.g. Refsnider *et al*., 2018; Lane *et al*., 2019). Finally, most *in situ* gradient studies focus on well-studied taxa, particularly plants and vertebrates, and as global datasets improve there should be excellent opportunities to broaden the taxonomic scope.

VI. Conclusions

1. SFTS is currently very widely used across subfields of ecology and evolution as a practical tool for generating urgent predictions of biotic responses to future climate change. Across the four subfields that we assess (population phenotypes, population genotypes, species distributions and ecological communities) there are many similarities in the approaches used, their strengths and their weaknesses.
2. Across the assessed subfields, the shared limitations that can undermine the robustness of SFTS inference relate to (i) correctly detecting causal climate-biotic relationships and (ii) the transferability of spatial climate-biotic relationships over time. We identify opportunities and best practice to address these limitations and improve the robustness 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 the four subfields and recognition of parallels in SFTS methods, limitations and innovations.
4. We anticipate that 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 robustness of projections.

VII. Glossary

Biotic lag: the biotic distance (e.g. Euclidian distance between phenotypic trait values) between the observed (or predicted) biotic state (e.g., phenotype, genotype or probability of species presence) under specific climate conditions and the predicted equilibrium biotic state for those conditions (Figure 3b). Also termed maladaptation, mismatch, disequilibrium, and climate debt.

Biotic offset: the biotic distance between the current biotic state (e.g., phenotype, genotype or probability of species presence) at a focal site and the predicted equilibrium biotic state at this site under future climatic conditions (Figure 3a; Fitzpatrick & Keller, 2015; Frank *et al.*, 2017). Where there is an immediate biotic response to climate change (e.g., via phenotypic plasticity), this results in a realised biotic offset. Our use of the term biotic offset is inspired by 'genetic offset' introduced by Fitzpatrick and Keller (2015), extended to generalise across biotic variables. Also termed vulnerability, risk of nonadaptedness, and (relative) risk of maladaptation.

Biotic response: a change in a biotic state, which can be driven by a change in climate. In this paper the main biotic variables we discuss relate to population phenotypes, population genotypes, species' distributions and ecological communities. We use the terms phenotypic response, genetic response, species' response and community response to refer to the specific biotic responses discussed.

Biotic state: a value of a biotic variable.

Climate-biotic relationship: the correlation between climate variable(s) and a biotic variable in space or time. We use 'climate-phenotype', 'climate-genotype', 'climate-species' and 'climate-community' relationships to refer more specifically to the biotic responses discussed.

Common garden transplants: organisms (i.e. individuals or communities) are moved into a shared 'common garden' environment (Figure 2b, Table 1bi). This includes when organisms are subjected to experimentally manipulated environments, with each treatment level being a common garden.

Distance of biotic lag: a biotic lag quantified in terms of spatial distance (Figure 3c, Table 1aiii). Where spatial and temporal data are both available, changes in climate and biotic responses over time can each be quantified in terms of a shift in spatial distance, and 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 variable (usually a species' presence/absence) with one or more environmental variables (usually including climate) in order to predict environmental suitability for the biotic states 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 single biotic state (Chase, 2003).

Exposure: the nature, magnitude and rate of climate change experienced by a biotic system (Foden *et al.* 2019).

***in situ* gradient approach:** spatial climate gradients are used to identify climate-biotic relationships (Figure 2a, Table 1a). This includes ecological niche models. Note that an *in situ* gradient could also refer to a gradient in time, but we use the term for spatial gradients alone.

Local adaptation: where spatially variable environments impose selection that maintains genotypic differences between locations, such that the fitness of local individuals tends to be greater than foreign individuals in their home 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 adaptation. These loci exhibit relationships with climate, but correlative methods do not prove that they are causally involved in adaptation.

Reciprocal transplant: organisms (i.e. individuals or communities) from different sites are moved into each other's environments so that the performance and/or traits (e.g., phenotype) of organisms experiencing local versus foreign and/or home versus away can be compared (Figure 2c, Table 1bii).

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

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

Space-time equivalence: an observation, inference or assumption that climate-biotic relationships in space and time are equivalent. This is a key assumption underlying SFTS and relates to the limitation of transferring of spatial climate-biotic relationships over time (Table 3b).

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 transplants or reciprocal transplants.

Vulnerability: the extent to which biotic systems are susceptible to the adverse effects of climate change (Foden *et al.* 2019).

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Table 1: Main space-for-time substitution (SFTS) approaches used in climate change ecology and evolution.

Method		**Purpose and Inference**	**Limits to inferences**
(a) *In situ* gradients approaches including ecological niche models (ENMs) Use of spatial climate gradients (e.g. latitudinal, altitudinal) to identify climate-biotic relationships	**(i) SFTS with a single or multiple predictor variable(s)** Estimate the climate-biotic relationship between one or more climate variable(s) and a biotic variable over space to make projections over time.	1. Climate-biotic relationships are assumed to capture causal effects, under the assumption that there are no unmeasured causal variables. Estimate can then be used to project biotic responses to a change in the focal climate variable(s) 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 in driving the biotic response and the relationship is sensitive to unmeasured variables. 2. Silent on the mechanisms of the biotic response to climate variables in space and whether the biotic response manifests over short or long timescales. 3. Assumes that current spatial patterns reflect the equilibrium (or in special cases optimum) relationship between the focal climate variables and the biotic variable.

(Figure 2a). This can then be used in a SFTS to make predictions about biotic responses over time.	**(ii) Space-time comparison** Estimate the climate-biotic relationship separately over space and over time and compare the direction and magnitude of the slopes. The spatial climate-biotic relationship is often assumed to capture the equilibrium (or in special cases the optimum) relationship.	1. Where the slope of the climate-biotic relationship 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 space-time equivalence validation – see section IV). 2. Where the estimated slopes of the spatial and temporal climate-biotic relationships 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	1. Particularly sensitive to unmeasured variables, as both the spatial and temporal climate-biotic responses may be affected (Tansey *et al.*, 2017), necessitating caution when drawing inferences. 2. Assumes that current spatial patterns reflect the equilibrium (or in special cases optimum) relationship between the biotic variable and the focal climate variables.

		reduces confidence that the climate variable is causal. 3. Spatial climate-biotic relationships are often assumed to capture the equilibrium (and in special cases the optimum) relationship. Therefore, where spatial and temporal climate-biotic relationships have slopes that 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.	

	(iii) Quantifying temporal change as distance Estimating the change in a climate or biotic variable over a spatial gradient and over time allows a temporal change to be translated into the spatial distance over which the equivalent change in the variable state 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 variable in a focal time period (Figure 3c). This ‘distance of biotic lag’ metric has the benefit of units (e.g. km) being easily interpretable and allowing multiple biotic variables to be compared on the same axis.	As above

(b) Transplants Moving organisms into different environments over *space* to provide insights into biotic responses to climate. Can be used to make predictions of biotic responses that may occur over *time.*	**(i) Common garden transplants** Organisms from two or more different sites are moved into a shared environment (a common garden; Figure 2b). This can be replicated along an environmental gradient and/or in an experimentally manipulated environment.	1. Comparing the biotic state at a home site to that at away (transplant) sites can reveal an immediate biotic response to environmental change (e.g. plasticity; Stamp & Hadfield, 2020). The immediate biotic responses to a specific climate driver can be estimated where (i) the climate variable(s) is/are manipulated across experimental replicates or (ii) replication of source sites permits correlation-based analysis of causal effects of climate variables. 2. Comparing the biotic states 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 garden transplants do not inform of the effects of specific climate drivers on biotic variables. 2. Differences among organisms in a common garden environment are not sufficient on their own to evidence spatial differences in equilibrium biotic state (e.g., local adaptation). 3. For some taxa, transplant experiments are impractical or even impossible.

		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 biotic responses to future climate change, assuming that climate is causal. This includes estimating biotic offsets (Figure 3a).	Therefore, the use of transplants is largely limited to taxa such as plants (e.g. Alexander *et al.*, 2015).

	(ii) Reciprocal transplants (sometimes called reciprocal common garden transplants) Organisms from different sites are moved into each other's environments allowing the performance (and biotic state) of local and foreign organisms at a site to be compared (Figure 2c).	1. Comparing biotic states in home sites to those at away (transplant) sites or under manipulated conditions can reveal an immediate biotic response to environmental change (e.g. plasticity; Stamp & Hadfield, 2020). 2. Comparing the biotic states 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	1. Where the focal environmental driver is not directly manipulated and replication is insufficient (i.e. a limited number of sites are considered), reciprocal transplants cannot reveal which environmental variables (including climate) drive biotic responses. 2. For some taxa, transplant experiments are impractical or even impossible. Therefore, the use of transplants is largely limited to taxa such as plants (e.g. Alexander *et al.*, 2015).

		aspects, e.g., phenotypes) to be attributed to spatial differences in the equilibrium 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 response is lagging behind the changing environment. 4. 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.	

		5. 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 biotic responses to future climate change, assuming that climate is causal. This includes estimating biotic offsets (Figure 3a).	

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

Subfield and example paper	**Method**	**Inference**	**Key assumptions**
(a) Population phenotypes **Wilczek *et al.* 2014 *PNAS***	Wilczek *et al.* transplanted seed banked accessions of *Arabidopsis thaliana* collected across Europe 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 the four sites.	At three of the four common garden sites, genotypes with origins that were local had higher relative fitness than those from other regions (foreign), suggesting the presence of local adaptation. However, for the most northerly common garden site (Finland), accessions originating from a historically warmer location had higher fitness than the home accessions. The authors suggest that this is	The conclusion that adaptation is lagging behind climate warming relies on the assumption that temperature is driving the among population variation in fitness (Table 3ai). However, other environmental variables may also exhibit similar patterns of variation across sites and so the causal variable is not robustly established.

		indicative of the historically collected accessions exhibiting a biotic lag to temperature.	
(b) Population genotypes **Bay *et al.* 2018** ***Science***	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 (temperature, precipitation, vegetation indices, tree cover, elevation and surface moisture). These contemporary associations were then used to predict genomic variation for a particular	The authors found that geographic regions with higher genomic vulnerability had experienced the largest population declines, and conclude that these populations are already being negatively affect by climate change.	The correlative approach to identifying climate-genotype relationships is prone to false positives (Table 1ai; Table 3a; Section III(2)). See Fitzpatrick, Keller & Lotterhos (2018b) for a discussion of specific limitations of this study. A subsequent simulation study has further shown that the observation of greater genomic vulnerability to future climates (biotic offset) in smaller populations is expected under genetic drift alone, and should therefore not be interpreted as evidence

	climate model for 2050. Geographic variation in predicted genomic vulnerability (i.e. biotic offset) was calculated as the Euclidean distance between contemporary and predicted genomic states.		that such populations are already maladapted to present climate (Láruson *et al.* 2022).
(c) Species distributions **Thomas *et al.* 2004 *Nature***	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 change in climatically suitable areas, the authors 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 climate and dispersal scenarios, and highlight the importance of minimising climate change.	This study relies on a number of key assumptions, as demonstrated by the high variability in the number of species 'committed to extinction' (9-52%). In particular, there is a lack of validation of both causality and transferability of models (Table 3), with the authors instead citing generic validation of ENMs, despite considerable variability in the transferability of ENMs across space, time, taxa and

			modelling methods (Jarnevich *et al.*, 2015).
(d) Ecological communities **Alexander *et al.* 2015 *Nature***	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 were found to have reduce the performance of focal plant species under increased temperatures (i.e. under the scenario where a species fails to migrate to track climate change) but had little effect under current temperatures (i.e. under the scenario where a species migrates to track the changing climate).	This study relies on the key assumption of causality: with only three common garden sites, it is impossible to demonstrate a causal effect of temperature on community composition (Table 3ai).

Table 3: General limitations of SFTS that apply across all four subfields (population phenotypes, population genotypes, species' distributions, ecological communities) and potential mitigations

Type of limitation	**Specific limitation**	**Improvements and Recommendations**
a) Causality Issues identifying causal climate-biotic relationships (i.e. where climate is driving the biotic response).	**i) Identification of causal climate predictors** Both the omission of causal variables and the inclusion of too many or non-causal predictor variables (i.e. overfitting) can bias SFTS estimates (Synes & Osborne, 2011; Beale & Lennon, 2012; Fourcade, Besnard & Secondi, 2018). Unmeasured causal variables could be other abiotic or biotic variables and their non-inclusion reduces our ability to accurately predict biotic 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).	1) Using biological knowledge to select climate variables that are likely to be causal (Elith & Leathwick, 2009), e.g., forcing temperature as a predictor of plant phenology. 2) Where the estimated slope of the climate-biotic relationship is similar across multiple gradients or types of gradients (e.g. altitudinal, latitudinal, urbanisation), this can increase or decrease confidence relationships have a causal basis (Loewen, *et al.* 2023). 3) Estimating the relationships between multiple abiotic (including climate) and biotic variables in space versus time

	Omitted causal variables are especially problematic for SFTS where correlations between the causal and non-causal variable differ in space and time (Tansey, Hadfield & Phillimore, 2017). Causal inference can also be problematic in transplant experiments, where '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.	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). 4) There are approaches for choosing drivers that could be shared between the four subfields. For example, phenotypic studies often focus on the seasonal timing over which a climate variable is important (Roberts, 2008; van de Pol *et al.*, 2016), whereas ENMs generally consider multiple climate variables and nonlinear climate-biotic relationships.
	ii) Appropriate sampling	1) Selective sampling of environments, such as stratified sampling or matching methods (Andam *et al.*, 2008), could

	A spatial sample may not capture the true relationship between variables, such as due to sampling biases or incomplete sampling. Additionally, if there is variation in the frequency of different climate conditions over space, this may result in unequal climate representation in the sample.	be used to generate a sample that is representative of the available climate conditions. 2) A greater emphasis should be placed on statistical power in study design, including selection of sampling locations that minimise the autocorrelation between predictor variables.
	iii) Spatial autocorrelation Spatial autocorrelation is ubiquitous in biotic and climatic data, with sites that are closer together being more similar. 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, *in situ* climate-biotic relationships 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 climate-biotic slope estimates toward zero. It is also possible for estimates of climate-biotic relationships to be biased away from zero when, as one moves toward more extreme climates, there is a greater tendency for	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 for predicting impacts on biotic states, we recommend that microclimatic modelling (Kearney *et al.*, 2020; Maclean, 2020) is used to generate 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

	organisms to use microclimates that are less extreme than coarser scale climate conditions. For example, microclimates can provide suitable climatic refugia for organisms, even when coarser scale climate conditions would render a site unsuitable (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).	recommend examining relationships between microclimates and coarser climate variables in both space and time to determine when this will be an issue. See also, recommendation a.i.3.
b) Transferability Issues relating to the transferability of spatial climate-biotic	**i) Lack of temporal validation** Models are often projected over time, under future (or past) climates, but their ability to accurately predict biotic changes over time is rarely assessed, due to a lack of testing data.	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, greater use could be made of existing historic data that have been underutilised for hindcasting,

relationships over time (Sequeira *et al.*, 2018; Yates *et al.*, 2018).		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 time to reach equilibrium precludes quantitative analysis, there may be potential to make qualitative predictions over shorter timescales amenable to validation tests. 4) Where suitable testing data are not available, there is still great value of using simulations to detect limits to inference (e.g. Zurell *et al.*, 2010; Qiao *et al.*, 2019; Adler *et al.*, 2020).

		5) Space-time comparison provides an opportunity to test whether climate-biotic relationships are of similar magnitude in space and time (Phillimore *et al.* 2010; Table 1aii).
	ii) Assumption of contemporary spatial equilibrium 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 biotic lag between the contemporary biotic state and the equilibrium biotic state for those climate conditions (Figure 3b); whether current spatial patterns are at equilibrium with the climate is unclear, variable across systems (Gaüzère *et al*., 2018), and largely untested.	1) Rather than using a single historical average for each climate variable at a site we suggest analysis of a sliding window of historical climate to identify the time period over which climate best predicts the system (van de Pol *et al.*, 2016). 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

	Recent anthropogenic shifts in climate may have perturbed many systems from their long-term equilibrium. There is potential for the climate-biotic relationship to be out of equilibrium in its intercept and/or slope. The consequences of either for SFTS predictions are unknown (Coulson, 2021). If a system is in a transient biotic 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, biotic 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 (introduction of alleles from other populations), and instead be at selection-migration equilibrium (Hadfield, 2016).	of temporal data. Therefore, we suggest that theory represents the most promising avenue for exploring the problems that non-equilibrium in the intercept and/or slope of the climate-biotic relationship 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 projections to understand how the transient biotic 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 biotic response Relationships observed over space are likely to be the result of both long-term and short-term processes, but the immediate temporal biotic responses that are more relevant to climate change predictions (i.e. over decades) will be mostly driven by short-term processes (Dunne *et al.* 2004; Adler *et al.*, 2020; Münzbergová *et al.*, 2021). Therefore, there may be a biotic lag in the temporal biotic response, with equilibrium not reached in the short-term or potentially not reached at all (Chevin, Lande & Mace, 2010). This biotic 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.	A method for quantifying the projected timescale for a biotic 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.

	iv) No-analogue climates In the future, organisms may be exposed to climatic conditions not experienced today, but models do not contain any information about biotic responses to these novel conditions and so rely on extrapolation (Williams & Jackson, 2007; 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 climate-biotic relationships. Tipping points may be reached.	1) Where possible, experiments can provide insights into biotic 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).