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Reconsidering space-for-time substitution in climate change ecology

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Ecologists often leverage patterns observed across spatial climate gradients to predict the impacts of climate change (space-for-time substitution). We highlight evidence that this can be misleading not just in the magnitude but in the direction of effects, explain why, and make suggestions for improving the reliability of ecological forecasts.

Climate influences the functioning of ecological systems, from the physiology and fitness of individuals to the dynamics of populations and species' distributions to the productivity, resilience and biogeochemical cycling of ecosystems. Because of the many benefits these ecological systems provide to humanity, including regulation of Earth's climate, predicting the ecological impacts of climate change is an urgent challenge. Space-for-time substitution (SFTS) is a strategy used to predict ecological responses to changing climate when long-term observations are lacking; prediction is instead based on patterns observed across spatial climatic gradients. We note that this form of SFTS differs from an analysis of sites at different successional stages (known as a chronosequence) where the term SFTS originated. The most prevalent use of SFTS is species distribution modelling, but SFTS has also been used to predict population carrying capacity, community composition and ecosystem productivity.

However, accumulating evidence casts doubt on the reliability of SFTS for predicting ecological responses to climate change. Using a spatial network of tree-ring time series for *Pinus ponderosa*, Perret et al.[1] showed that trees grow faster at warmer locations but slower in warmer-than-average years (Fig. 1a,b). Thus, SFTS forecasting suggests trees should benefit from warming (Fig. 1c), whereas the tree-ring data showed that trees suffered in response to warming. The SFTS forecast was misleading not just in magnitude, but in sign. Opposite responses to spatial versus temporal climate variation have been found in the growth of other tree species[2,3], grassland productivity[4], pathogen-driven forest mortality, demography of herbaceous plants, and bird abundance, suggesting this pattern is not uncommon (reviewed in refs. 1,3 and 5). Negative effects of warming throughout a species' entire range[1–3,6] also contradict the expectation that individuals at the cool edge of species' distributions should benefit from warming, that is, 'leading edge' range expansion.

We focus here on two reasons why SFTS predictions can be misleading – namely, assumptions embedded in SFTS (Fig. 2a). The first is causality[7]. SFTS is based on regression, hence the familiar phrase 'correlation is not causation' applies. Although spatial variation in climate can be statistically associated with an ecological variable such as a species' occurrence or ecosystem productivity, this does not mean that climate is its only determinant (Fig. 2a, *y* axis). The risk of misattribution

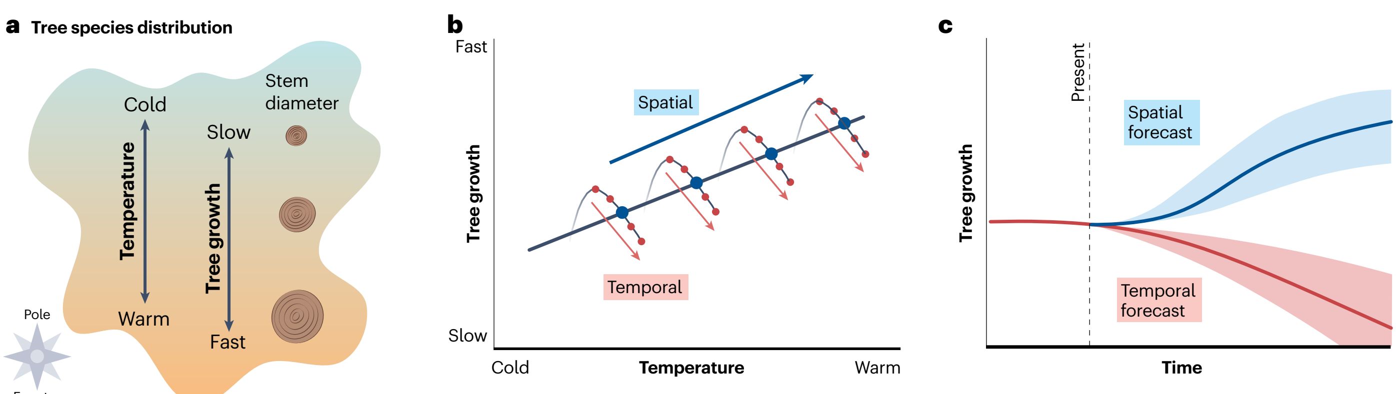

Fig. 1 | Opposite responses to spatial versus temporal variation in temperature have been documented in several spatial networks of tree-ring time series. **a**, Across the geographic distribution of tree species, average growth rate is often faster at warm locations (orange shading) compared to cool locations (blue shading)[1–3]. **b**, Blue points indicate this spatial regression pattern. Red points indicate the response of individual trees within a population to variation in temperature across time (years): lower growth rate in warmer-than-average years. Each black curve represents a thermal performance curve, fading to grey to indicate the part of the curve not observed in the wild. **c**, Predictions of future tree growth based on spatial regression (SFTS) versus time-series regression are opposite in sign.

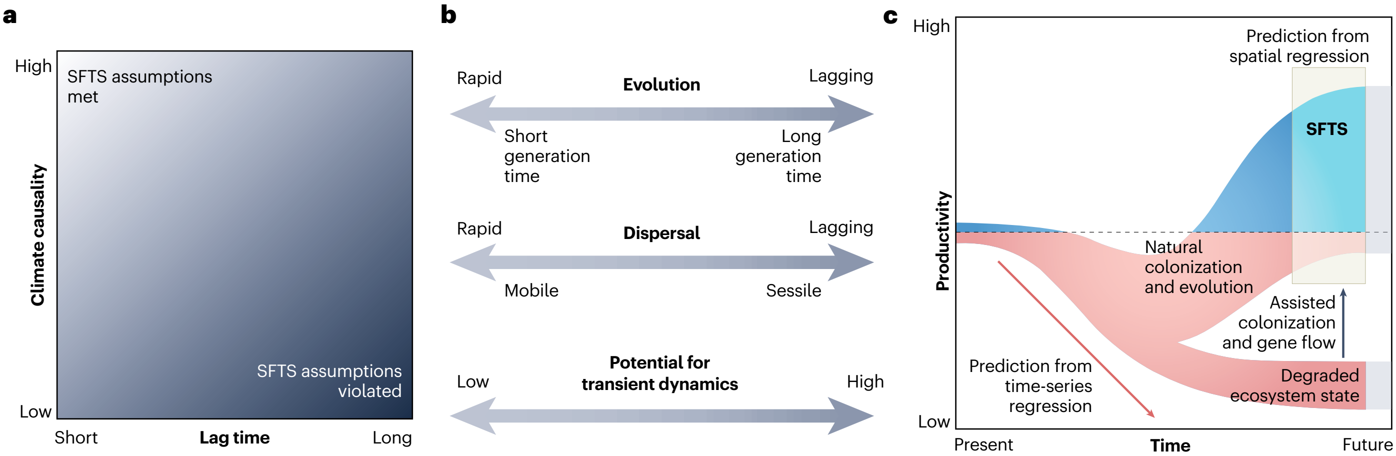

Fig. 2 | Reasons why SFTS may generate misleading predictions of ecological response to climate change. a, Two implicit assumptions underpin SFTS. The first (*y* axis) is that spatial climate variation alone causes spatial ecological patterns (or that correlations between climate and other causal factors will not change in the future). The second (*x* axis) is that the ecological response does not lag behind changing climate. **b**, Two examples of ecological processes that can generate a lagged response are evolutionary adaptation and dispersal, with examples of life history characteristics that influence lag time. The potential for transient dynamics increases with lag time. **c**, Example of an ecological variable (forest productivity) showing a lagged response to warming, with contrasting transient versus equilibrium dynamics. The historical baseline level of forest productivity is indicated with a horizontal dashed line. A gain in productivity relative to this baseline is indicated with blue shading; a loss of productivity in indicated with red shading. A negative impact of warming on forest productivity (and carbon sequestration) is predicted in the near term, based on regression of time-series data. A positive impact of warming on forest productivity is predicted in the long term, based on SFTS (spatial regression), but reaching that long-term expectation requires evolutionary adaptation (of thermal tolerances) or colonization by better-adapted genotypes or species, either naturally or via assisted colonization and gene flow. Panel **c** adapted from ref. 5 under a Creative Commons license CC BY 4.0.

is particularly heightened in an era of abundant spatial data and flexible regression techniques (machine learning and artificial intelligence) that excel at matching patterns. SFTS can alternatively be viewed as using climate as a proxy for additional causal factors, with the assumption that correlations between climate and those other factors will not change. Both assumptions are likely to be frequently violated.

The second reason SFTS can be misleading is that ecological responses often lag behind climate change (Fig. 2a, *x* axis). Organisms, communities and ecosystems adjust to climate variability and change via processes that operate on timescales from very fast (physiological acclimation, plastic expression of traits and demographic outcomes) to slow (evolutionary adaptation, dispersal of genotypes or species, changes in community composition, and changes in soil characteristics or biogeochemical cycling)[2,3,5,8]. Patterns inferred across spatial climate gradients tend to reflect the influence of slow in addition to fast processes; they represent equilibrium expectations of the relationship between climate and the ecological system or variable[2,3,5,8]. Anthropogenic climate change is outpacing some of these slower processes, generating lagged responses and transient dynamics that are not reflected in SFTS forecasts (Fig. 2b).

Contrasting transient versus equilibrium ecological dynamics, evidenced by contrasting responses to spatial versus temporal variation in climate, can have societally important consequences. As a case in point, the signatories to the Paris Agreement collectively plan to rely on forests to meet 25% of their greenhouse gas emissions reduction goals, making it critical to accurately predict forest ecosystem carbon dynamics. SFTS prediction of forest productivity (hence carbon dioxide drawdown) would suggest a positive response to warming, whereas the response observed from tree-ring time series is negative across much of the temperate and boreal zones[1–3,6]. Recovery of tree- and ecosystem-level productivity requires in situ evolution, dispersal of better-adapted genotypes from elsewhere, or colonization by better-adapted species, either naturally or via human intervention, such as assisted gene flow or assisted colonization (Fig. 2c). Thus, transient dynamics can lead to permanent or quasi-permanent undesirable outcomes such as the loss of ecosystem function or biodiversity. Failing to account for these transient dynamics could, in the example case of forest-based natural climate solutions, lead to missed emissions reductions or carbon storage goals.

Given the emerging evidence that SFTS predictions can be misleading, we advocate for more diverse approaches to forecasting and a focus on improved forecast reliability via uncertainty analyses and model validation (Fig. 3). A first step is to qualitatively assess the assumptions that underpin SFTS and whether they are likely to be violated in the study system, given the targeted forecast horizon[8,9] (Fig. 3, first node). As a rule of thumb, SFTS should be reliable if there is a strong causal relationship between climate and the variable being predicted, and if ecological processes do not lag behind the pace of climate change (Fig. 2a) or if the forecast horizon is long relative to the pace of lagging processes. For example, SFTS predictions are more likely to be reliable in study systems where evolution and dispersal (or other potentially lagging processes) are rapid, such as a microorganism or insect with a short generation time compared with a long-lived tree, or a mobile organism compared with a sessile organism[9] (Fig. 2b).

If the assumptions of SFTS are not unambiguously met, we recommend estimating the uncertainty surrounding SFTS forecasts (Fig. 3). A relatively low-effort exercise is to bound forecast uncertainty caused by potentially lagging processes using contrasting ('data free') scenarios (Fig. 3, path 2). Such uncertainty reporting has long been common in species distribution modelling using scenarios of unlimited versus

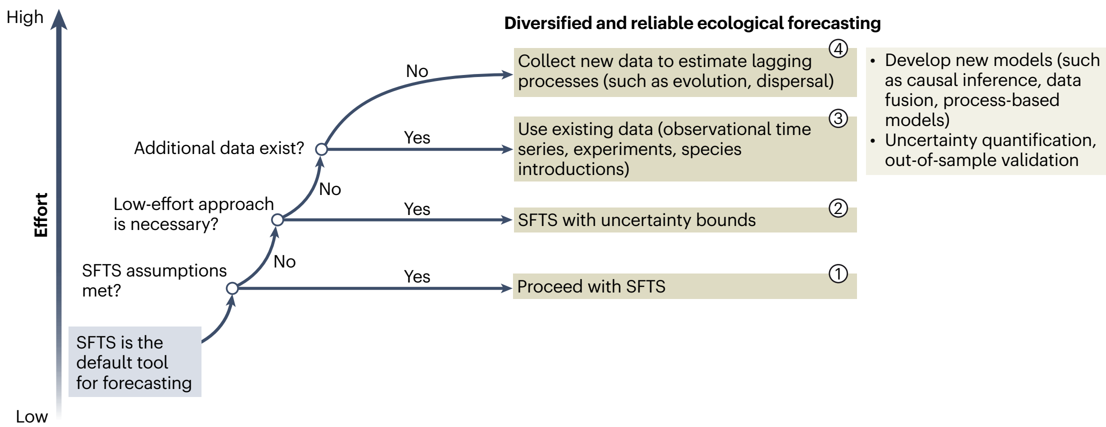

Fig. 3 | A roadmap towards diversified and more reliable ecological forecasting. In the lower left is the status quo: SFTS is the default approach. Nodes are labelled with questions to guide forecasting choices, starting with a qualitative assessment of whether SFTS assumptions are met in the study system. If yes, forecasting can proceed with SFTS (path 1). If these assumptions are likely to be violated, but a low-effort approach is needed, SFTS can be accompanied by scenario-based uncertainty reporting (path 2). If resources are available that support greater effort, existing complementary data can be leveraged (path 3), or new data can be collected (path 4). On path 3 or 4, forecast reliability can be increased through uncertainty quantification, out-of-sample model validation and modelling alternatives to spatial regression.

no dispersal. A similar approach could be taken to put bounds on the role that evolution could play in constraining species' range change, that is, using scenarios of no local adaptation to climate (and/or rapid evolution) versus strong local adaptation (and/or slow evolution). A next level of effort is to compare climate sensitivities estimated from spatial versus temporal datasets[4]; if spatial and temporal climate sensitivities are consistent, then uncertainty is much lower. Comparing forecasts based on different data types is a further step towards quantifying forecast uncertainty. Regardless of the approach taken, there currently exist many data sources that can be creatively leveraged to evaluate how violations of SFTS assumptions might change forecasts, including observational time series, common garden experiments[10,11], climate manipulation experiments, botanical gardens, species' introductions, and resurrection studies (Fig. 3, path 3).

In addition, increased effort should be put into validating SFTS forecasts (Fig. 3), beyond cross-validation that divides spatial data into model training versus testing subsets. Validation can and should take many other forms: the use of time-series data for hindcasting[1] or change validation[12], iterative near-term forecasting that compares model predictions to newly collected data[13], and a variety of forms of out-of-sample validation using independent data[14]. Data sources available for such forecast validation include the BioTIME (https://biotime.st-andrews.ac.uk/) and BioDeepTime (https://biodeeptime.github.io/) databases, biodiversity surveys and community science initiatives, monitoring of natural resources such as forests, fisheries and rangelands, natural archives (for example, pollen, tree rings and otoliths), long-term experiments, and accumulating remotely sensed data (Fig. 3, path 3). If validation statistics for SFTS forecasts are low[1,12,14], further investigation is needed to determine whether low climate causality or transient dynamics are the reason.

Finally, greater effort and resources should be directed at generating new data that fill knowledge gaps (for example, time series, experimental and genetic; Fig. 3, path 4) along with new modelling approaches. Research is needed that quantifies the timescales of potentially lagging processes (for example, empirical estimates of local adaptation, evolutionary potential and gene flow) to understand whether evolutionary adaptation may constrain species' persistence in the face of climate change[9,15]. Development of forecasting approaches that use causal inference or process-based models, or fuse data with complementary spatial and temporal characteristics (for example, remotely sensed and ground observations) in models, will help diversify the forecasting toolbox.

The use of SFTS for ecological forecasting has long been justified as sufficiently accurate or the only approach fit for the task given the higher data needs of alternative strategies. However, SFTS carries a heavy assumption burden: that climate is the only driver of ecological change (or correlations between climate and other drivers will not change) and that ecological systems will instantaneously equilibrate with changing climate. Recent work suggests violation of these assumptions yields predictions that are far from 'good enough', that is, directionally misleading. It is time to reconsider SFTS. Explicit interrogation of the assumptions underpinning SFTS and more diverse approaches to ecological forecasting – with uncertainty reporting, forecast validation and the creative use of existing and new data – will improve the reliability of ecological forecasts that underpin policy, management and mitigation of the climate and biodiversity crises.

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Competing interests

The authors declare no competing interests.