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Research

Impacts of climate timescale on the stability of trait–environment relationships

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Summary

- Predictive relationships between plant traits and environmental factors can be derived at global and regional scales, informing efforts to reorient ecological models around functional traits. However, in a changing climate, the environmental variables used as predictors in such relationships are far from stationary. This could yield errors in trait–environment model predictions if timescale is not accounted for.
- Here, the timescale dependence of trait–environment relationships is investigated by regressing *in situ* trait measurements of specific leaf area, leaf nitrogen content, and wood density on local climate characteristics summarized across several increasingly long timescales.
- We identify contrasting responses of leaf and wood traits to climate timescale. Leaf traits are best predicted by recent climate timescales, while wood density is a longer term memory trait. The use of sub-optimal climate timescales reduces the accuracy of the resulting trait–environment relationships.
- This study concludes that plant traits respond to climate conditions on the timescale of tissue lifespans rather than long-term climate normals, even at large spatial scales where multiple ecological and physiological mechanisms drive trait change. Thus, determining trait–environment relationships with temporally relevant climate variables may be critical for predicting trait change in a nonstationary climate system.

Introduction

Climatic factors like temperature, atmospheric aridity, and water availability strongly impact the strategies by which plants grow, allocate resources, and respond to stress (e.g. Woodward, 1987) – and, consequently, their traits (e.g. Wright *et al.*, 2004; Messier *et al.*, 2010; Reichstein *et al.*, 2014). Understanding relationships between plant traits and their environment, particularly via predictive trait–environment relationships that can be directly derived from trait observations (e.g. Boonman *et al.*, 2020), can help to elucidate how climate shapes the distribution and diversity of vegetation at the global scale (Lavorel & Garnier, 2002; Wright *et al.*, 2005; Laughlin, 2014). While such relationships have myriad applications in trait-based ecology, including flexibly parameterizing large-scale ecological models (e.g. Verheijen *et al.*, 2013, 2015; Famiglietti *et al.*, 2023), as well as extrapolating between sparse *in situ* data (Borgy *et al.*, 2017), their potential utility is hampered by their relatively low predictability (Anderegg, 2023).

Indeed, there is ample evidence that underlying relationships between traits and climate exist across a range of scales. Responses of leaf traits such as leaf mass per area (LMA) and leaf nitrogen content (LNC) – both of which correlate to photosynthetic capacity (Field & Mooney, 1986; Niinemets, 1999) – to climate factors are particularly well-studied. For example, results from a synthesis of laboratory studies examining trait change within species indicate inverse relationships between LMA and either temperature or water availability (i.e. leaves become thicker and denser as the local climate cools or dries), as well as a positive relationship with radiation (Poorter *et al.*, 2009). Relationships between leaf traits, such as LMA and LNC, and climate are also modulated by changes in light availability (Niinemets *et al.*, 2015; Keenan & Niinemets, 2016). On longer timescales and larger ecological scales, drought, elevated carbon dioxide, nitrogen deposition, and increasing temperatures have each been linked to shifts in leaf traits via climate manipulation experiments (Saban *et al.*, 2019; Cui *et al.*, 2020), regional meta-analyses (Wellstein *et al.*, 2017), globally distributed *in situ* measurements (Madani *et al.*, 2018), optimality theory (Smith *et al.*, 2019; Smith & Keenan, 2020), earth system model simulations (Doughty *et al.*, 2018), and remote sensing data analyses (He *et al.*, 2017; Dong *et al.*, 2022). Beyond leaf traits, other plant organs are also strongly affected by climatic variability. Tree-ring studies indicate that the density of wood, for instance, responds to environmental effects – notably temperature and water availability – on both intra- and inter-annual timescales (Parker & Henoch, 1971; Bouriaud *et al.*, 2005). Among-species and among-community patterns in wood density also respond to climate (Chave *et al.*, 2006; Bruelheide *et al.*, 2018), though often less strongly than to soil fertility (Chave *et al.*, 2009). Taken together, such trait responses may even induce broader feedbacks within the climate system. Leaf trait acclimation to elevated carbon dioxide, for instance, may amplify warming through reductions in evapotranspiration (Kovenock & Swann, 2018). Widespread changes in albedo that have global climate impacts may also result from trait shifts in tundra ecosystems caused by species turnover (Sturm *et al.*, 2005; Swann *et al.*, 2010; Myers-Smith *et al.*, 2011).

However, climate change is inducing pervasive shifts in the environmental covariates that affect plant behavior over time (e.g. Hughes, 2000; Dai, 2013), and at rates that may outpace organisms' abilities to re-equilibrate to new conditions (Loarie *et al.*, 2009; Schimel *et al.*, 2013). Thus, a growing mismatch may exist between distributions of key plant traits and climate dynamics of the present and recent past (Cui *et al.*, 2020), which could yield errors in trait–environment model predictions if they are based on climate records not representative of the timescale at which that trait actually responds to climate. Addressing this source of error is not straightforward, though. First, there is no agreed-upon temporal span to be used for climate predictors in the development of trait–environment relationships. Most prior work simply uses the entirety of the relevant climate data record available (e.g. Ordoñez *et al.*, 2009; Verheijen *et al.*, 2013). For example, while a recent study by Boonman *et al.* (2020) presented global distributions of specific leaf area (SLA; the inverse of LMA), LNC, plant height, and wood density based on relationships between traits and climate, no temporal dimension was considered in the models, and reliable predictions of LNC could not be achieved. Second, it is unclear over what timescales different plant traits respond to past climatic controls – and whether these response timescales are static or dynamic, as well as species- or trait-specific. The multiple physiological and ecological drivers of trait change (e.g. lineage or species turnover, changes in species abundance, and trait acclimation within species) make it very difficult to predict *a priori* which timescales may be relevant for any given trait (Anderegg, 2023). These unresolved questions suggest that neither the stability nor consistency of trait–environment relationships across time are well-understood, underscoring potential limitations of their generalizability (e.g. Anderegg *et al.*, 2018; Yang *et al.*, 2019). The role of timescale may further restrict the strength and universality of such relationships, which are already challenged by the overwhelming diversity of vegetation behavior within and between species, communities, and biomes (Bruelheide *et al.*, 2018; Anderegg, 2023).

Here, by regressing thousands of globally distributed trait measurements from the TRY database (Kattge *et al.*, 2020) on several increasingly extensive records of local climate characteristics, we investigated two questions. First, what – if any – is the optimal timescale with which trait distributions are predicted by climate factors? Second, how much do derived trait–environment relationships change as a function of climate (predictor) memory? We focus on three traits for which strong links to the environment have been demonstrated previously (Verheijen *et al.*, 2013; Butler *et al.*, 2017; Walker *et al.*, 2017; Boonman *et al.*, 2020): SLA, LNC, and wood density. These traits are well-suited to this analysis not only because of their previously demonstrated trait–environment relationships, but also because of the large number of measurements publicly available for modeling and their relevance for understanding multiple dimensions of plant functioning.

Materials and Methods

Overview

Using several thousand globally distributed *in situ* measurements of SLA, LNC, and wood density aggregated within 9 km pixels, we derived predictive relationships between these plant traits and local climate variables. The choice of the 9 km pixel size was based on the resolution of the climate data. We considered a range of 'climate integration times' – spanning 30–1 yr before the measurement date – to evaluate both the predictive strength and temporal consistency of these relationships as a function of timescale. Throughout this paper, the phrase 'climate integration time' is used to refer to the time period over which summary climate statistics are calculated. Our methodology is represented schematically in Fig. 1.

Trait measurements

The TRY database is a comprehensive, publicly accessible archive of plant trait measurements across the globe (Fraser, 2020; Kattge *et al.*, 2020). From TRY, we downloaded all public records of SLA (including those with petiole included or excluded), mass-based LNC, and wood density. For each trait, we removed measurements with insufficient metadata. Specifically, we required that all measurements contained a geolocation and a sampling year equal to or after 1980 (30 yr past the start of the climate data record). Following filtering methods used by Boonman *et al.* (2020), we also required that (1) measurements were taken only from natural vegetation rather than managed systems; (2) sampled species were representative of the broader plant community or dominant vegetation structure growing at that location; and (3) measurements were not obtained from early successional communities or from seedlings or juveniles. After implementing these filters, we retained 35 281 measurements of SLA, 12 288 measurements of LNC, and 5753 measurements of wood density.

Due to the variability in development and life history between species with different growth forms (e.g. Santiago & Wright, 2007), we further subdivided the remaining measurements into two classes: woody (trees and shrubs) and nonwoody (herbs and grasses). However, because of sample size restrictions on the nonwoody class, we restricted the remainder of our analysis only to the woody class (> 5× more woody than nonwoody measurements). To categorize each species as woody or nonwoody, we referred to the growth form dataset provided by Engemann *et al.* (2016), which synthesizes information from several sources, including Wright *et al.* (2010). Approximately 77% of the filtered TRY measurements were directly matched with

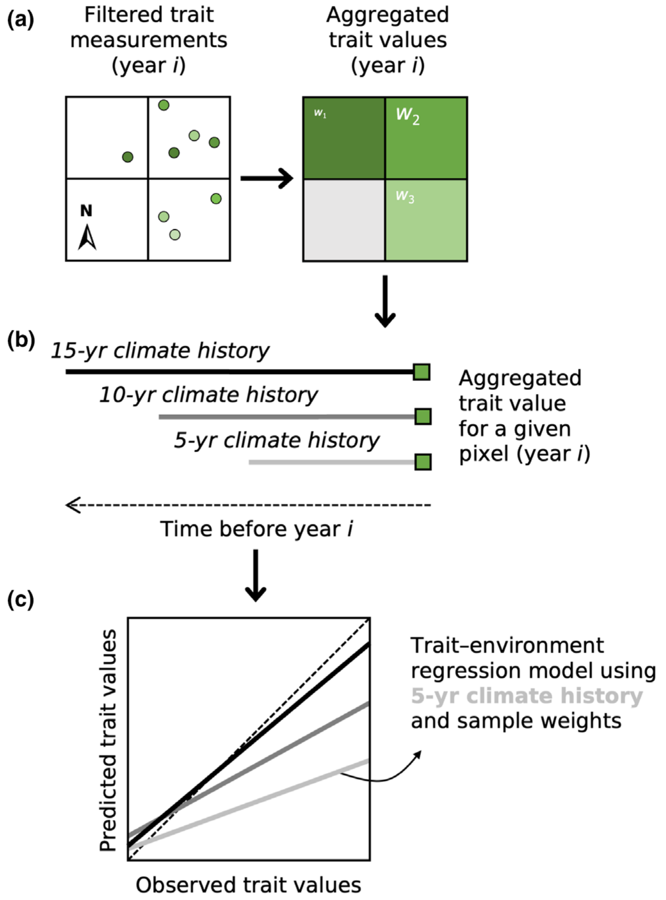


Fig. 1 Schematic representation of workflow, including (a) aggregation of the filtered trait measurements within 9 km pixels; (b) calculation of predictors across climate integration times; and (c) trait–environment regression models using different climate histories. In (a), sample weights corresponding to the square root of the number of measurements per pixel are represented by $w_2 > w_3 > w_1$.

species included in the Engemann *et al.* (2016) dataset. In cases when a given species was not included in the dataset, but other species from that genus were included (*c.* 20% of measurements), we assigned the most common listed growth form for that genus to the unlisted species. If no species from that genus were included in the Engemann *et al.* (2016) dataset (*c.* 3% of measurements), we conducted web and literature searches for species-specific growth form information. No information could be found for < 0.1% of measurements, most of which were missing relevant metadata. These measurements were removed from the analysis.

Finally, we aggregated the remaining *in situ* trait measurements to align with the 9 km spatial resolution of the climate variables. To do so, for each trait, we isolated all the woody, species-level measurements that fell into a given pixel for a given sampling year (Supporting Information Figs S1–S3). Because the filtering criteria described above ensure that individual measurements are representative of the broader community or dominant vegetation structure (Boonman *et al.*, 2020), we took a simple average of these measurements for further modeling and analysis.

Climate data

We used climate data from the land component of the fifth-generation European ReAnalysis dataset (ERA5-Land) from the European Centre for Medium-Range Weather Forecasts (ECMWF), which provides high resolution (9 km) information about land surface meteorology, water, and energy cycling from 1950 to present (Muñoz-Sabater *et al.*, 2021). We downloaded all available ERA5-Land data for the following variables at the monthly timescale: 2 m air temperature, total precipitation, soil water content (0–7 and 7–28 cm depths), and downward surface solar radiation. We also downloaded 2 m dew point temperature data, which we used to calculate the vapor pressure deficit (VPD). These variables were selected because they have previously been shown to be predictive of plant traits (e.g. Verheijen *et al.*, 2013; Butler *et al.*, 2017).

For each pixel-year, we then extracted local climate summary metrics over several different climate integration times. These ranged from 30 to 1 yr prior to the aggregated trait value. Specifically, for each environmental covariate, we calculated the overall mean as well as the standard deviation of monthly averages (hereafter referred to as the seasonality) across the entire record. These values were considered as predictors in the regression models for each trait. We used a two-sample Kolmogorov–Smirnov test to evaluate whether the 30- and 1-yr distributions of each climate predictor at the sampled pixels are significantly different. The statistical test returns the Kolmogorov–Smirnov statistic, *D*, which represents the maximum distance between the two cumulative distribution functions, and a corresponding *P*-value.

Trait–environment regression models

We developed multiple linear regression models for each combination of trait and climate integration time to test the hypothesis that trait–environment relationships shift as a function of timescale. These models were of the following form:

$$\left(y=\sum_{j=1}^{n} a_j X_j + b\right)_{i,t} \qquad \text{Eqn 1}$$

where y is the predicted trait value; a_j are the regression coefficient values for each of n climate predictors X_j; b is the intercept; $i \in (1, 30)$ is the climate integration time; and $t \in$ (SLA, LNC, wood density) is the trait. Before regression analysis, each X_j was rescaled between 0 and 1; trait values were log-transformed due to their significant skew; and each sample (pixel value) was weighted using the square root of the number of trait measurements within that pixel. Overall, the regression coefficient value a_j corresponding to a given environmental covariate X_j reflects the magnitude and directionality of its impact on the predicted trait y. These models were implemented in PYTHON using Scikit-Learn's LinearRegression functionality.

Climate predictor selection

For every trait, we chose a subset of the 12 potential predictors prior to making model predictions. This was intended to reduce multicollinearity and mitigate equifinality (which, in this context, is the case in which different combinations of predictors could yield the same result).

First, we removed highly cross-correlated predictors from the models ($r > |0.75|$). For each plant trait studied, we identified all groups of cross-correlated predictors at the sampled pixels (Figs S4–S6) and retained only the predictor most strongly correlated to the target trait within each group (the other predictors were removed from the analysis). After this step, seven predictors with $r \leq |0.75|$ remained for SLA and LNC, while five predictors remained for wood density. Note that cross-correlations were assessed only at the sampled pixels, which varied from trait to trait.

We then conducted an analysis using Bayesian information criteria values (BIC, a common method for scoring a model that takes complexity and sample size into account) to select the most parsimonious set of predictors from those remaining (Figs S7–S9). This ensures that predictors adding only a relatively small amount of value to the model are not included, thereby reducing the potential influence of equifinality and noise on the analysis. This approach yielded three final predictors for each trait.

Analysis

To answer our first research question (*what – if any – is the optimal timescale with which trait distributions are predicted by environmental factors?*), we assessed the skill of the trait-specific regression model predictions as a function of climate integration time and identified performance optima. Skill was measured using the coefficient of determination (R^2), weighted root-mean-square error (wRMSE), weighted mean absolute percentage error (wMAPE), and weighted mean absolute error (wMAE). All metrics were weighted according to the sample weights used for model development (square root of the number of trait measurements per pixel; Fig. 1).

Trait predictions are a direct function of which (and how many) pixels were sampled along with their weights, as well as which (and how many) predictors were included in the regression framework. To characterize the range in skill resulting from the limited sample size, we implemented a statistical bootstrapping procedure that randomly resamples pixels (and associated predictors) with replacement prior to regression. Second, to characterize the range in skill resulting from the choice of predictors, we conducted recursive feature elimination, which uses feature importance rankings to remove predictors one at a time until a specified number of predictors is reached. We performed recursive feature elimination several times for each trait, testing every possible number of predictors less than the size of the final set.

To answer our second research question (*how much do derived trait–environment relationships change as a function of predictor memory?*), we evaluated feature importance rankings derived via recursive feature elimination as well as the degree to which the regression coefficient values shift across the different climate integration times, using the standard error σ_j on each coefficient as a measure of significance.

Results

Shifts in climate across integration times

Consistent with our expectation of a changing climate, the summary metrics used as predictors in the trait–environment regression models shift across climate integration times. Specifically, by comparing distributions of each predictor variable between the longest (30-yr) and shortest (1-yr) integration times, we find statistically significant increases in shortwave radiation, mean temperature, and VPD at the sampled pixels, as well as decreases in average total precipitation and soil water content (Fig. 2). The seasonalities of both soil water content layers also increase markedly when comparing recent to historical climate, and the largest shift of any variable occurs for the seasonality of shortwave radiation (Fig. 2b). The seasonalities of temperature and VPD appear relatively stable across integration times, although their shifts are still statistically significant. Overall, these shifts in climate are not spatially uniform but instead show latitudinally variable patterns (Fig. S10), potentially leading some individual trait measurements to derive from organisms experiencing stronger shifts in climate than are captured by global summaries alone. Taken together, this evidence of climate change at the sampled pixels between the 30- and 1-yr integration times demonstrates the importance of evaluating whether trait–environment relationships developed using different climate histories are inconsistent and/or unstable.

Optimal climate integration time for trait–environment prediction

When comparing the resulting trait predictions for woody plants across the full suite of tested integration times, the three traits show different performance optima (Fig. 3). SLA is best predicted by short integration times – that is, by recent climate. Specifically, the quality of SLA predictions (measured through the coefficient of determination, R^2) improves when moving from 30- to 1-yr integrated climate, which is its optimal integration time (Fig. 3a). Furthermore, a notable upward spike in skill occurs *c.* 4 yr prior to the measurement. Similarly, LNC, which is physiologically linked to SLA through relationships with photosynthetic capacity, is also optimally predicted with recent (1 yr) rather than historical climate (Fig. 3b). The predictability of LNC as a function of timescale is slightly more stable than that of SLA, showing only marginal increases in R^2 when the optimal rather than other integration times are used. We tested the hypothesis that this insensitivity may result from weaker shifts in climate at the pixels where LNC was sampled than at the pixels where SLA or wood density were sampled, but did not find strong evidence to support this (Fig. S11). We also repeated the analysis using only datasets that measured at least two traits at the same time, finding consistent results (Fig. S12).

Wood density shows different behavior than the two leaf traits when considering variations in skill across integration times. Its optimal climate integration time extends 7 yr before the measurement (Fig. 3c). In general, higher quality wood density

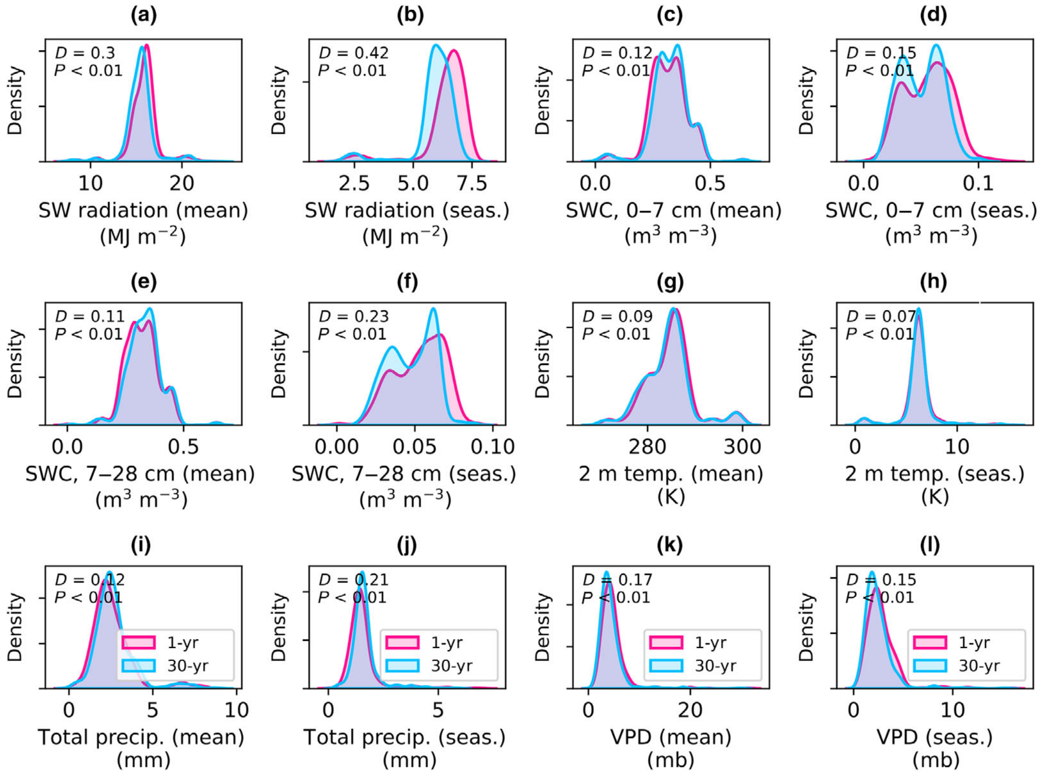
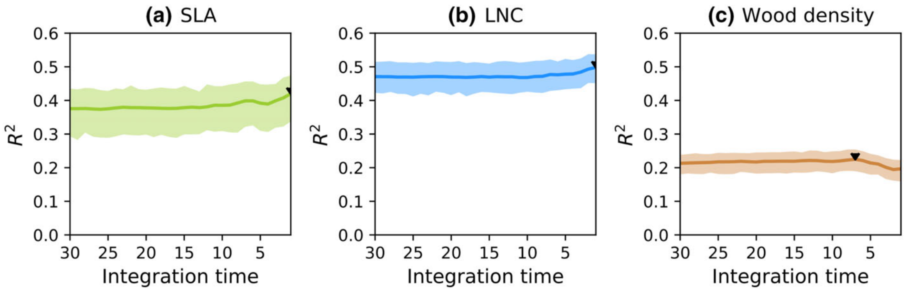


Fig. 2 Distributions of climate variables at the sampled pixels for 30- and 1-yr integration times. The Kolmogorov–Smirnov statistic, which represents the maximum difference between cumulative distribution functions, is denoted by *D*.

Fig. 3 Relationship between predictive skill (coefficient of determination, R^2) and climate integration time for (a) specific leaf area (SLA), (b) leaf nitrogen content (LNC), and (c) wood density. Black triangles indicate each trait's performance optimum, and shading corresponds to sampling uncertainty. Behavior of only woody plants is modeled.



predictions are generated with longer integration times, and a substantial decline in skill is observed when using climate histories shorter than 7 yr.

Overall, using the R^2 metric, SLA and LNC are the best-predicted traits (Figs 3, S13). The optimal model for SLA (using 1-yr integrated climate predictors) explains 42% of variance and is closely followed by that for LNC, which explains 50% of variance using 1-yr integrated climate predictors. Wood density is more challenging to predict, achieving only 22% variance explained using its optimal (7-yr) climate integration time. However, the R^2 values of the SLA and LNC predictions are slightly more uncertain than those of wood density predictions (Fig. 4). This result holds when considering sampling uncertainty (quantified via bootstrapping and shaded in Fig. 3) as well as predictor space composition (quantified via recursive feature elimination, whereby we evaluated models with successively fewer predictors). Both span a larger range for the two leaf traits than for wood density.

The consequences of deriving trait–environment relationships with sub-optimal climate timescales persist across multiple error metrics (Fig. 5). For all three traits, wRMSE, wMAPE, and wMAE are minimized – though each with a large range in possible values from bootstrapping – when the optimal integration time is used. In the case of LNC and particularly for SLA, errors are comparably larger when using longer rather than shorter sub-optimal integration times. For wood density, increases in error are marginal, but are most apparent when using 1-yr (too-short) integrated climate predictors.

Stability of trait–environment relationships across integration times

With this improved understanding of optimal integration time, its uncertainty, and its variability across traits, we next investigated the degree to which underlying relationships between

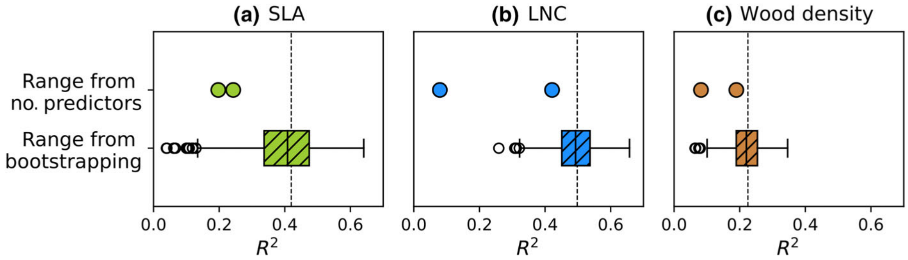


Fig. 4 Range in predictive skill at the optimal integration time resulting from trait measurement sampling (shown in boxplots) and predictor space composition (shown in filled circles) for (a) specific leaf area (SLA), (b) leaf nitrogen content (LNC), and (c) wood density. The horizontal line represents the median; the whiskers extend from the lower to upper quartile; the open circles are outliers (beyond the IQR).

predictors and the target trait shift across models driven by different climate integration times. Indeed, the concept of timescale dependence includes not only variations in predictability across integration times, but also extends to the ways in which traits and climate are linked when considering different temporal domains (i.e. which climate predictors best predict trait values).

In Fig. 6, we present discrete relative importance rankings for each predictor variable across traits and integration times (the highest ranking indicates the strongest predictor of that trait). In Fig. 7, we present the corresponding regression coefficient values underlying those rankings for a selection of integration times. We found that the relative importance rankings of the predictors show differences in stability as a function of trait and climate integration time (Fig. 6), although shifts in regression coefficient values all remain within the range of standard errors (Fig. 7). First, all predictor rankings in the SLA and LNC models remain stable across integration times. Mean VPD, average total precipitation, and the seasonality of 2 m temperature are consistently the top three predictors of SLA (Fig. 6a). Similarly, mean VPD and the seasonalities of shortwave radiation and 2 m temperature are consistently the most important predictors of LNC (Fig. 6b). For both leaf traits, the coefficient value for mean VPD shrinks

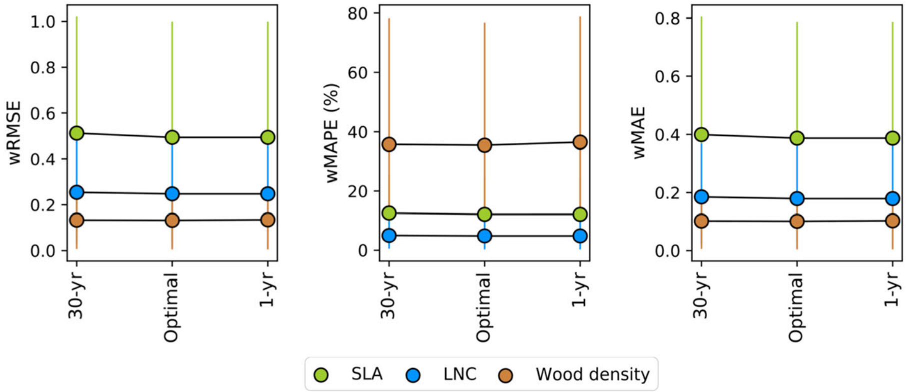


Fig. 5 Error comparison for all trait predictions using longest (30-yr), shortest (1-yr), and optimal integrated climate predictors. Vertical bars correspond to bootstrapping uncertainty.

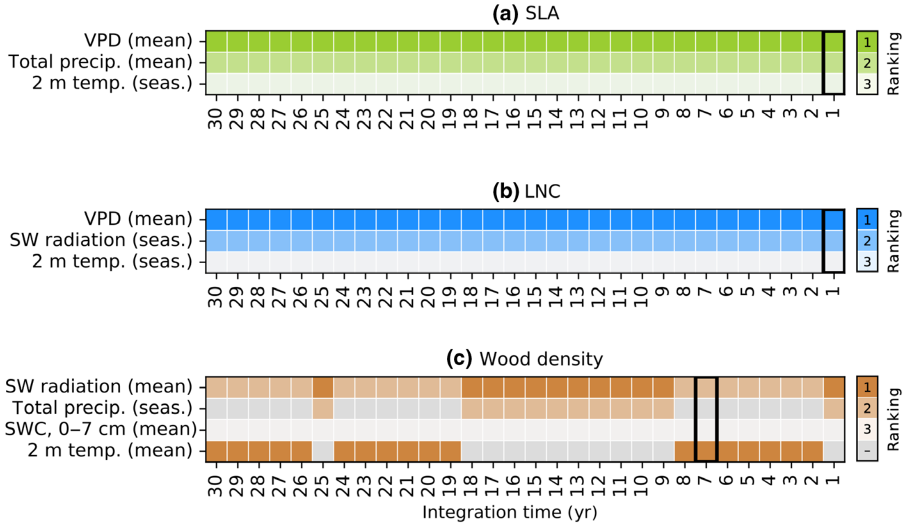


Fig. 6 Predictor importance rankings resulting from recursive feature elimination for (a) specific leaf area (SLA), (b) leaf nitrogen content (LNC), and (c) wood density across integration times. For each trait, the optimal integration time is highlighted with a thick black outline. Colors correspond to importance rankings, with darker colors representing higher rankings. Gray colors in panel (c) represent a predictor that was not selected in that model.

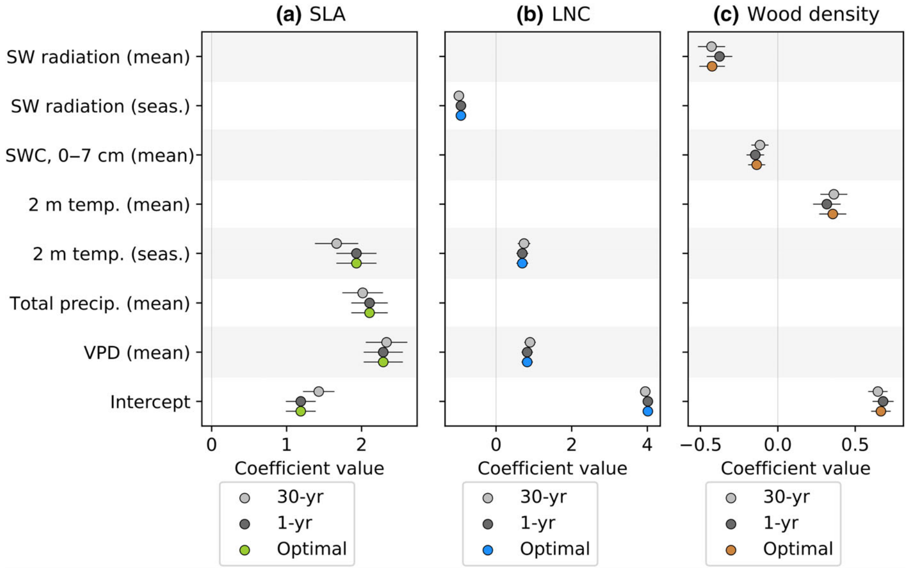


Fig. 7 Regression coefficient values and SEs for trait–environment relationships developed using 30-yr (light gray), 1-yr (dark gray), or optimal (colored) integrated climate predictors. Each panel corresponds to a different trait: (a) specific leaf area (SLA), (b) leaf nitrogen content (LNC) and (c) wood density.

slightly when the optimal integration time is used rather than the longest one (2% decrease in coefficient value for SLA; 9% decrease for LNC), while the coefficient value for temperature variability increases by 16% for SLA and decreases by 7% for LNC (Fig. 7a,b).

By contrast, substantial variability in importance rankings is observed in the wood density model (Fig. 6c). Mean temperature and mean radiation are each just as likely to be the top predictor of wood density at different integration times, with temperature outweighing radiation at the optimal integration time. Precipitation variability is also an important predictor of wood density, but only at mid-range climate timescales.

Discussion

Physiological controls on the timescale dependence of trait–environment relationships

The challenge of predicting plant traits with environmental factors given the astounding ecological diversity of the terrestrial biosphere (Bruelheide *et al.*, 2018) is further complicated by the existence of optimal climate integration times, which we demonstrate vary from trait to trait at the global scale. Signals of this dependence on climate timescale can be directly inferred from publicly available trait measurements.

Understanding the biological basis of these relationships with climate timescale is necessary in order to draw a clearer picture of trait–environment predictability and its limitations. In particular, several mechanisms may explain the variability in optimal integration times we identified between different traits (Fig. 3). The relatively short residence time of foliar carbon (Bloom *et al.*, 2016), as well as the ability of plants to dynamically adjust their leaf traits, such as SLA, on seasonal to diurnal timescales in response to environmental perturbations (Poorter *et al.*, 2009; Dwyer *et al.*, 2014; Keenan & Niinemets, 2016), may contribute to the greater predictability of leaf traits by recent climate compared with historical climate. LNC is also highly plastic, demonstrated in part through its variability in different light environments (Rozendaal *et al.*, 2006). This can be explained by the fact that photosynthetic infrastructure and associated photosynthetic processes, which plants can adjust on short timescales, depend on N-rich enzymes (e.g. Stitt & Schulze, 1994; Reich *et al.*, 1997). By contrast, tree-ring development – and accordingly wood density, which showed a longer timescale dependence than either SLA or LNC in our study – reflects changes in temperature, water availability, and other environmental controls integrated over the entire lifetime of the organism (Zobel & van Buijtenen, 1989; Roderick & Berry, 2001). Indeed, wood density captures the influence of many xylem growth rings – each of which represents only 1 yr of growth – while leaves (in deciduous species) regrow annually.

Regression coefficient stability and consistency with previous studies

Wood and leaf traits differ not only in their timescale dependencies but also in the variable stability of their underlying relationships with climate factors, which we interpreted in part via regression coefficient sensitivities. We caution, though, that because these sensitivities are derived from multiple linear regression models (i.e. they represent partial rather than univariate correlations), they should be interpreted in concert rather than independently. Furthermore, despite removing the most strongly cross-correlated climate predictors from our models and selecting a parsimonious model via BIC, it is still possible that some degree of multicollinearity impacts our interpretation of these environmental sensitivities.

In the wood density model, all coefficient shifts remained within the standard error of the corresponding 30-yr value (Fig. 7c) despite variability in importance rankings across integration times (Fig. 6c). Our results indicate a consistent positive relationship between mean temperature and the target trait as well as inverse relationships associated with mean soil water content and radiation. The signs of these sensitivities to temperature and water availability match findings from studies of field plots (Bouriaud *et al*., 2005). The contrasting sensitivities of wood density to mean radiation (negative) and mean temperature (positive) were somewhat unexpected, though, as the two are typically linked and increases in either variable could stimulate photosynthetic activity and growth in the absence of water or nutrient limitations (Bouriaud *et al*., 2004). Additionally, Boonman *et al.* (2020) found strong impacts of minimum temperature, precipitation in the driest quarter of the year, and soil cation exchange capacity on wood density. Though the exact formulation of the predictor variables used here differs from the aforementioned study, we also identify temperature and water availability as important predictors of wood density (Fig. 7c).

By contrast, greater stability in predictor–target relationships was observed in both leaf trait models across climate integration times. While coefficients for mean VPD and the seasonality of temperature (the two traits common to both the SLA and LNC regressions) were more sensitive to integration time for SLA than for LNC, no shifts in coefficient values were greater than their standard error and the signs of the retrieved predictor–target relationships remained the same, regardless of integration time (Fig. 7a,b). For the leaf trait models, only some – but not all – of the underlying coefficient relationships aligned with expectations. For instance, we found a positive effect of mean total precipitation on SLA. In their study of trait–environment relationships for parameterizing global vegetation models, Verheijen *et al.* (2013) found inverse relationships between water availability (mean annual precipitation) and SLA for some vegetation types. However, Swenson *et al.* (2012) reported the opposite in a global synthesis of woody plant traits. We also identified a positive effect of VPD on both leaf traits (Figs 6a,b, 7a,b). In a review of experimental studies with varying VPD treatments and plant growth environments, López *et al.* (2021) reported significantly increasing LNC with increasing VPD (consistent with our results), but weakly decreasing SLA with increasing VPD (unlike our results). Relatedly, Boonman *et al.* (2020) identify the aridity index as the strongest predictor of SLA and the second-strongest predictor of LNC in their study of global trait–environment relationships, though the signs of these relationships are positive (a lower aridity index yields lower leaf trait values).

Taken together, we find varying degrees of consistency between our predictor–target relationships and those reported in the literature across traits. This range of agreement may be explained by the difficulty of comparing trait–environment relationships across scales (e.g. experimental or climate manipulation studies vs measurements from natural vegetation; site-scale studies vs vegetation type-specific subsets vs global aggregations; and so on). This challenge is compounded by issues related to trait measurement sampling (e.g. representativeness of sampled species given variations in community structure and composition between different ecosystems), which functional groups are included in the analysis (e.g. only woody plants here vs woody and herbaceous plants in other analyses), and specific methodological choices relating to model structure and development (e.g. exactly which predictors were considered as potential descriptors of each trait; the degree to which model parsimony was prioritized; and the impact of equifinality between predictors; Fig. 4).

Implications for trait distributions under future climate change

The trait-specific environmental sensitivities identified here suggest that shifts in climate strongly affect vegetation behavior and support the idea that a rapidly changing climate may induce disequilibria in global distributions of plant traits (Aitken *et al*., 2008; Schimel *et al*., 2013). In fact, signals of this disequilibrium are already apparent. For example, Hill *et al.* (2023) found evidence for a growing vegetation–climate mismatch in California's Sierra Nevada mountains marked by increasingly unsuitable environmental conditions for conifer regeneration, which may cause increased vulnerability to disturbance and increased likelihood of species turnover. This acceleration falls within the larger backdrop of differential velocities of climate change across the global land surface – species are facing increasing pressures to 'keep up' with shifts in environment (Loarie *et al*., 2009; Corlett & Westcott, 2013). The relatively long optimal integration time of wood density (Fig. 3), which may be explained by responses to water stress, suggests that wood density and other traits linked to plant water use are more likely than short-term memory traits to be in such disequilibrium with climate. However, it is also possible that the climate timescale dependencies and associated optimal integration times of different plant traits will continue to evolve with climate change, complicating our ability to project trait distributions and associated environmental sensitivities into the future.

Recommendations for trait-based modeling

Efforts to integrate trait-based methodologies into ecological models of many scales – including those describing plant growth (Enquist *et al*., 2007), community assembly (Laughlin & Laughlin, 2013), species distribution (Violle & Jiang, 2009), and dynamic global vegetation (van Bodegom *et al*., 2012) – are becoming increasingly common. Limitations to the generality of such trait–environment relationships, such as the trait-specific optimal climate integration times identified here, are salient to these modeling efforts. Here, we present three key lessons from our investigation into climate timescale that are generalizable across trait-based modeling approaches.

(1) *There is no 'one-size-fits-all' trait–environment relationship.* The choice of integration time may have greater consequences for some trait predictions than others (e.g. compare LNC to wood density in Fig. 3). Still, it is clear that arbitrary, trait-invariant climate timescales are insufficient to reliably capture the broad spectrum of trait variability across the globe. Indeed, we identified two classes of traits – 'short-term memory' (here, SLA and LNC) and 'long-term memory' traits (here, wood density) – which showed contrasting performance optima (Fig. 3) and different dynamics of coefficient (in)stability. Accordingly, trait–environment relationships, including climate integration time and the composition of the predictor space (e.g. number and type of climate variables; Fig. 6), should be tailored to the individual trait of interest. Even in situations where consideration of trait-specific climate integration times is not considered practical or feasible, though, our results still suggest that integration times < 10 yr are more appropriate than the multi-decade integration times often used in past trait–environment relationship studies.

(**2**) *Multicollinearity and equifinality should be considered during model development.* Trait–environment relationships are prone to equifinality, which is the situation in which different (potentially unphysical) coefficient combinations yield the same result (Beven & Freer, 2001). One reason for this susceptibility is the high degree of cross-correlation between climate predictors (Figs S4–S6), leading to potential misattribution of model sensitivities when this multicollinearity is not accounted for. While introducing a greater number of predictors can be important in order to adequately characterize a given trait–environment relationship when the initial predictor space is very small (e.g. only one or two predictors; Figs 4, S7–S9), the resulting equifinality may lead to uncertainty in the coefficients of the trait–environment relationship and incorrect interpretations of which predictors are most strongly linked to the target trait (Figs 6, 7). Extensive analysis of predictor cross-correlations and/or interdependencies, as well as a careful choice of the number of necessary predictors, is therefore recommended. For example, results from our analysis with BIC (Figs S7–S9) suggest that the use of more than three or four predictors may yield diminishing returns.

(**3**) *Trait–environment predictions should be made using the same climate integration times with which the relationship was developed.* A mismatch in climate integration times used during relationship development vs upon application may restrict accuracy, robustness, and interpretability. Such a mismatch could occur if a trait–environment regression equation derived in one context (e.g. with some set of trait measurements and climate predictors) is used to make predictions in another, independent context (e.g. to parameterize an ecosystem model). Consider the wood density model in our study, while prediction quality remained relatively consistent at all but the shortest few integration times (Figs 3c, 5), the composition of the predictor space varied significantly across the integration time axis (Fig. 6). Thus, as long as the choice of integration time is consistent between development and application, the effect of climate timescale may be mitigated. If it is not, however, variability in underlying coefficients may lead to unexpected behavior.

Remaining uncertainties

While we have identified clear trait–environment timescale dependencies using a relatively simple regression framework, our approach contains several imitations. We acknowledge that sampling- and species-related biases of these trait measurements contribute substantial uncertainties to our models, though this is far from inconsistent with prior trait–environment work (Anderegg, 2023). Indeed, the greater predictability of both SLA and LNC than wood density observed here may first be a function of the representativeness of the trait measurements used for relationship development. As shown in Figs S1–S3, SLA and LNC are much more widely sampled across space and time in the TRY database than wood density is, potentially enabling more underlying variability to be explained by the regression models.

Additionally, the complete spectrum of environmental factors relevant to trait variability was not tested here, nor were the impacts of using different integration times for different climate predictors within the same regression model. Future studies should pursue such an analysis, but it is outside the scope of this paper, which is a proof of concept seeking to align as closely as possible with existing modeling approaches. Because our focus was on climate variables that evolve on annual to decadal timescales, we also neglected the role of slow-evolving environmental covariates such as edaphic factors (Hulshof & Spasojevic, 2020), which are also known to influence plant behavior. Indeed, the soil cation exchange capacity and soil pH were shown as relevant predictors of SLA, LNC, and wood density by Boonman *et al.* (2020). By not including these properties, our approach prioritized predictor space simplicity with the goal of mitigating equifinality. The inclusion of information about soil texture yielded only marginal improvements in prediction accuracy for some traits (most notably wood density, for which R^2 at its optimal integration time increased from 0.22 to 0.28; Fig. S14). Nonetheless, the skill of our predictions is comparable to recent work by Boonman *et al.* (2020), in which SLA, LNC, and wood density were predicted with average R^2 values of 0.24, 0.12, and 0.32, respectively.

Third, our analysis only reflects relationships between woody plants and climate, which does not capture the full spectrum of global vegetation behavior. A detailed analysis by individual plant growth form or functional type is challenging for several reasons, including inconsistent metadata accompanying trait measurements; biases in the growth forms of commonly measured species (Sandel *et al.*, 2015); and limited species-level information in growth form databases (e.g. Engemann *et al.*, 2016). Our focus on only woody species was a direct function of data availability. Nonetheless, optimal integration times of nonwoody plants (which remain to be investigated) are also relevant for understanding the full spectrum of vegetation responses to climate.

Fourth, we derived relationships using trait measurements from the TRY database, which – while exceptionally valuable – are sparse and spatially nonuniform. The degree to which these sparse measurements are representative of the total diversity of terrestrial ecosystems across the globe is limited (Schimel *et al.*, 2015), and our point-to-pixel aggregation could lead to uncertainties, especially in highly heterogeneous locations. Furthermore, different measurements may have been sampled at different times of year, which could bias results for fast-evolving leaf traits. Looking forward, opportunities for novel monitoring and observation of species distributions and ecosystem function are becoming increasingly accessible. In particular, hyperspectral remote sensing for functional trait estimation can avoid the limitations and difficulties of on-the-ground measurement in a scalable and repeatable way (e.g. Asner *et al.*, 2015; Wang *et al.*, 2020). Still, given that remote sensing approaches cannot capture individual-scale behavior, broad and repeated *in situ* sampling remains necessary and critically important.

Conclusions and paths forward

Trait-specific dependencies on climate integration time represent an under-explored limitation on the generalizability and universality of trait–environment relationships. However, developing a robust understanding of these effects remains complicated by the multiple interacting ecological and physiological mechanisms driving trait change across scales and by the limited data available to characterize them. Looking forward, an improved understanding of optimal climate integration times for trait–environment predictions may help guide intelligent restoration, conservation, or management efforts (e.g. Sandel *et al.*, 2011; Carlucci *et al.*, 2020; Merchant *et al.*, 2023), given that vegetation resilience to environmental change is modulated by trait variability (Liu *et al.*, 2023). Such an improved understanding could also increase confidence in future ecological projections (e.g. Madani *et al.*, 2018) and inform trait-based modeling efforts across scales (e.g. Famiglietti *et al.*, 2023).

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Competing interests

None declared.

Author contributions

CAF and AGK conceived and designed the study. CAF implemented the experiments and wrote the code used for modeling and analysis. CAF led the interpretation of the results with input from MW, LDLA, and AGK. CAF wrote and revised the manuscript in consultation with MW, LDLA, and AGK.

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Data availability

The data underlying this study are publicly available via the TRY database (trait IDs: 3115, 3116, 3117, 14, 4). These data are accessible at https://www.try-db.org/.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Number of specific leaf area measurements per pixel per year, colored by latitude.

Fig. S2 Number of leaf nitrogen content measurements per pixel per year, colored by latitude.

Fig. S3 Number of wood density measurements per pixel per year, colored by latitude.

Fig. S4 Pairwise Pearson correlations for all candidate climate predictors in the specific leaf area model.

Fig. S5 Pairwise Pearson correlations for all candidate climate predictors in the leaf nitrogen content model.

Fig. S6 Pairwise Pearson correlations for all candidate climate predictors in the wood density model.

Fig. S7 Bayesian information criteria values across integration times for specific leaf area models with different numbers of predictors.

Fig. S8 Bayesian information criteria values across integration times for leaf nitrogen content models with different numbers of predictors.

Fig. S9 Bayesian information criteria values across integration times for wood density models with different numbers of predictors.

Fig. S10 Average shifts in climate between 1- and 30-yr integration times within 10-degree latitude bands.

Fig. S11 Shifts in climate between 1- and 30-yr integration times, partitioned by trait.

Fig. S12 Skill across integration times for specific leaf area, leaf nitrogen content, and wood density when only including publications/sub-datasets that measured more than one trait.

Fig. S13 Observations vs predictions made using each trait's optimal climate integration time.

Fig. S14 Range in predictive skill at the optimal integration time when soil factors are included in the regression models.

See also the Commentary on this article by Cui, **241**: 2313–2315.