Climate sensitivity and ecoclimate sensitivity: theory, usage, and past implications for 21st-century biospheric responses

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ABSTRACT

Two usages of 'climate sensitivity' co-exist: one climatological, one ecological. The earlier climatological usage quantifies the sensitivity of global mean surface temperature to atmospheric CO_2, with formal variants differing by timescale and processes. The ecological usage, renamed here as ecoclimate sensitivity, is defined as a change in an ecological response variable per unit climate change. The two concepts are treated very differently: climatologists have focused on reducing uncertainty of global climate sensitivity estimates, while ecologists have focused on the multivariate processes governing variations in ecoclimate sensitivity across drivers, response variables, and scales. Because radiative forcing scales logarithmically to $[CO_2]_{atm}$, ecological impacts per ppm $[CO_2]_{atm}$ often also scale logarithmically, although non-linear ecoclimate sensitivities can alter this expectation. Critically, past estimates of climate and ecoclimate sensitivity carry an implicit tradeoff, in which smaller estimates of climate sensitivity indicate higher ecoclimate sensitivities. For the LGM, estimates of equilibrium climate sensitivity have narrowed to 2.4 to 4.5°C, while high ecoclimate sensitivity is indicated by post-glacial biome conversions, continental-scale species range shifts, and high community turnover. We introduce a new term, ecocarbon sensitivity, defined as the product of global climate sensitivity, local ecoclimate sensitivity, and a global-to-local climate scaling factor. Given past biospheric transformations, we can expect high sensitivity of the terrestrial biosphere to current rises in $[CO_2]_{atm}$, a conclusion that is insensitive to estimates of climate sensitivity. The next frontier is better quantification of the processes governing the form and variations of ecoclimate and ecocarbon sensitivity across systems and scales.

KEY WORDS

Climate sensitivity, Ecocarbon sensitivity, Ecoclimate sensitivity, Last Glacial Maximum, Paleoclimatology, Paleoecology

DECLARATIONS

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1. INTRODUCTION

How sensitive is the climate system to changing concentrations of atmospheric CO_2 ($[CO_2]_{atm}$) and other greenhouse gases, and how sensitive are ecological systems to changes in climate? These essential – yet very different – questions currently both fall within the common term of 'climate sensitivity.' Climatologists use climate sensitivity to refer to the sensitivity of global mean temperature to changes in $[CO_2]_{atm}$, with several formally defined variants that differ by timescale and included Earth system processes. Conversely, ecologists and other environmental scientists use climate sensitivity to refer to the sensitivity of ecological systems to changes in temperature, precipitation, and other climate variables, with an emphasis on understanding the variations in sensitivity in space and time. To minimize semantic confusion, we retain unchanged the climatological usage of 'climate sensitivity' and rename the ecological usage to 'ecoclimate sensitivity.' We use the Last Glacial Maximum (LGM) as a case study to show how several essential but underappreciated points emerge from the joint consideration of climate and ecoclimate sensitivity, particularly when using networks of paleoclimatic and paleoecological proxy data to understand biospheric responses to rising $[CO_2]_{atm}$ and 21st-century climate change.

Both questions have deep intellectual roots. The climatological usage traces to late 19th- and early 20th-century estimates by Arrhenius and Callendar [1] of the rise in global mean temperature that would result from a doubling of $[CO_2]_{atm}$. Efforts to define and estimate climate sensitivity more precisely accelerated after the Charney report [2] (Fig. 1), which estimated an equilibrium climate sensitivity (ECS) of 1.5 to 4.5°C per doubling of $[CO_2]_{atm}$. Since then, 'climate sensitivity' has become a central focus for climatologists, for assessing the performance of Earth system models (ESMs), and for discussions between scientists and policymakers, with trillions of dollars at stake [1,3,4]. ECS uncertainty has been central to these climate change debates, with battles fought at the margins of uncertainty. For example, 'lukewarmists' invoke lower-end ECS estimates to argue that climate change over the 21st century will neither be very large nor its impacts very severe, so that little action should be taken to stabilize atmospheric greenhouse gas concentrations, whereas climate hawks have focused on the risks of catastrophic impacts associated with higher-range ECS. Recent papers based on the latest generation of ESMs report widened ranges of 1.8 to 5.6°C ECS [5], while syntheses based on paleoclimatic data and models report narrowed estimates, e.g. 2.2 to 4.3 95% CI ECS [6,7] or 2.3 to 4.7°C 95% CI [for a closely related 'effective climate sensitivity' 8].

The foundations for ecoclimate sensitivity were emplaced also in the 19th century, when von Humboldt pioneered the co-location of meteorological measurements and botanical observations to demonstrate that species' distributions varied predictably along elevation (temperature and moisture) gradients [9,10]. Since then, generations of biogeographers, ecologists, paleoecologists, and evolutionary biologists have sought to understand how temperature and other environmental variations in space and time influence the evolution, distribution, and diversity of life [11,12]. However, the growth of 'climate sensitivity' in the ecological literature has lagged the climatological usage by approximately three decades (Fig. 1). This usage lag likely derives from the lag in the detectability of Earth system responses; climatologists first had to demonstrate that the climate system is detectably sensitive to anthropogenic greenhouse gas emissions. Now, as anthropogenic climate change intensifies, global-change ecologists are assessing the patterns of ecoclimate sensitivity, determining the

governing processes affecting rates of ecosystem change (e.g. effects of population demography, trophic position, or intra-range position), and using these scientific insights to inform climate adaptation strategies [e.g. 13,14-17] (Table S1). Assessments of ecoclimate sensitivity can help guide ecosystem managers by offering a useful quantitative metric to identify particularly sensitive species, processes, or systems [13,18-20]. Unlike climatology, there has been no attempt to identify a global mean ecoclimate sensitivity, due to the known variations in ecoclimate sensitivity across systems, scales, space, and time [21,22]; the many possible ecological response variables; and the non-linearity of many ecological sensitivity functions [e.g. 23,24,25].

Because of the large and correlated past variations in $[CO_2]_{atm}$ and temperature [26,27], paleoclimatic proxy data offer one of the best avenues for estimating ECS and constraining Earth system models [3,6 ,28,29]. The LGM is of particular interest because both GHG forcings and temperature changes are large and well constrained by observations [6 ,8,28,30,31]. Global proxy-based paleoclimatic reconstructions draw upon a wide array of physical, geochemical, and biological indicators [e.g.6,32-34], with biological proxies a backbone of many global paleoclimatic reconstructions and constraints on climate sensitivity [e.g. 29]. In parallel, paleoecologists and global change ecologists use the LGM and other past time periods to assess the sensitivity of species and ecosystems to past climate change [35,36], test the predictive ability of ecological forecasting models [37], and understand the dynamics of ecological systems responding to changing climates. These analyses support a high sensitivity of ecological systems to climate change, given the large post-glacial range expansions [38,39], large shifts in elevational distributions worldwide, widespread ecosystem-type conversions, and high local community turnover when rates of temperature change are high [35,40-42]. However, estimates of ecoclimate sensitivity vary among scales and dimensions of biodiversity [43]. For example, although contemporary levels of species richness and endemism appear to be highest in areas of climate and biome stability [44-47], yet species richness at continental to global extents appears to have been largely insensitive to global glacial-interglacial climate variations [48], except for the late-Quaternary megafaunal extinctions, at least some of which are likely also linked to the pressures of expanding human populations worldwide [49-51].

As we show below, several important points emerge from the joint consideration of climate and ecoclimate sensitivity, particularly when drawing inferences from the geological record about biospheric responses to 21st-century climate change. First, the ecoclimate sensitivity literature is younger and less developed than the climate sensitivity literature, with more work needed to establish a common conceptual framework and terminology for studying climate sensitivity. Second, scaling: because of the log-linearity of radiative forcing responses to $[CO_2]_{atm}$, ecological responses to $[CO_2]_{atm}$ should also be expected to scale logarithmically, hence the 95 ppm increase from the LGM to the Industrial Revolution is ecologically at least as significant as the ~135 ppm increase from the pre-Industrial period to present. Third, the potential risk of circularity: the same fossil data cannot be used to assess both climate and ecoclimate sensitivity. This risk of circularity grows as data assimilation methods advance to combine paleoclimatic proxy networks with ESMs to produce joint inferences of past climates [6,52]. The fourth and last issue is deeper and largely unrecognized: for past time periods where $[CO_2]_{atm}$ is known precisely (i.e. the last 800,000 years), there is an inverse relationship between

paleoclimatic estimates of climate sensitivity and paleoecological estimates of ecoclimate sensitivity. Therefore, smaller estimates of climate sensitivity for, say, the LGM directly imply a larger ecoclimate sensitivity, and vice versa.

To develop this argument, we first review the climatological definitions of climate sensitivity, drawing upon prior reviews [1,3,27], and add our own review of the recent literature on ecoclimate sensitivity and its usage. We use the LGM as a case study to: 1) show how proxy-based paleoclimatic reconstructions for the LGM have constrained ECS estimates, 2) briefly review the evidence for large climate-driven ecological changes from the LGM to present, and 3) demonstrate the inherent tradeoff between past estimates of climate and ecoclimate sensitivity. We then show how this tradeoff can be avoided in a simple theoretical framework that establishes ecocarbon sensitivity as a new concept, defined as ecological response per ppm $[CO_2]_{atm}$ and calculated as the product of climate sensitivity, ecoclimate sensitivity, and a scaling factor that connects local to global climate changes. As estimates of climate sensitivity narrow and as ecoclimate sensitivity grows as a focal area of research [e.g. 53,54,55], the next major frontier is to better estimate the patterns and processes governing ecoclimate and ecocarbon sensitivity across ecological systems and spatiotemporal scales.

2. CLIMATE SENSITIVITY – CLIMATOLOGICAL DEFINITIONS AND ESTIMATES

2.1 Definitions

The climatological and geological definitions of climate sensitivity are well established elsewhere [1,3,4,27] so here we briefly summarize key elements. The heat energy and temperature of the surface Earth system are governed by solar radiative forcing to the Earth system and feedbacks within the Earth system, with geothermal contributions negligible. Hence, changes in the externally imposed radiative forcing (ΔF) or internal feedbacks through changes in temperature and outgoing longwave emissions ($\lambda \Delta T$) will change the total heat energy in the surface Earth system (ΔQ):

$$\Delta Q = \Delta F - \lambda \Delta T \qquad \text{(Eq. 1)}$$

In this formulation, λ is the climate feedback factor, defined as the ratio of altered radiative forcing (via increased outgoing longwave radiation) to equilibrium temperature change, with units of W m^{-2} °C^{-1}. Its inverse, **S′**, is the **climate sensitivity parameter**, expressing the amount of surface temperature rise per change in external radiative forcing, with units of °C (W m^{-2})$^{-1}$ [1].

Equilibrium climate sensitivity (ECS) is defined as the change in global mean annual temperature produced by a doubling in $[CO_2]_{atm}$ [3,4, Box 12-2], which equates to a 3.7 W m^{-2} increase in radiative forcing. Note that Eq. 1 is linear, while ECS is log-linear because of band saturation effects, in which increasing greenhouse gas concentrations decrease the per-molecule effectiveness of greenhouse gases in absorbing infrared radiation [56]. If the Earth is treated as a simple blackbody, the expected warming for a doubling in $[CO_2]_{atm}$ is 1.2°C [1]. However, feedbacks within the Earth system mostly amplify the sensitivity of surface temperatures to $[CO_2]_{atm}$ [4,57]. Because many feedbacks operate within the Earth system, across a wide range

of timescales, both the feedbacks and timescales must be specified in order to have a meaningful and comparable estimate of climate sensitivity [27]. Hence, several standard definitions of climate sensitivity now exist, each with an explicit timescale and included processes [3]. Most definitions of ECS use the original Charney [2] definition, which focuses on 'fast' Earth system processes that were numerically represented in the ESMs of the late 1970s: changes in water vapor content; changes in lapse rate; and changes in albedo resulting from changes in cloud, snow, and ice cover. Even when just these processes are considered, the timescale for global temperatures to reach equilibrium is mostly governed by the thermal inertia and mixing rate of the world oceans, and so is on the order of millennia. The ECS and its Charney form have been the primary focus of most syntheses of climate sensitivity [1,3,4].

At shorter timescales, the **Transient Climate Response** (TCR) is defined as the change in global mean temperature after a 70-year period given a sustained 1% annual increase in $[CO_2]_{atm}$ [4]. However, because this definition can only be attained in ESM experiments with prescribed forcings, the TCR is more generally defined as the change in temperature per change in radiative forcing, during the time window before the deep ocean reaches thermal equilibrium [3]. Hence, TCR can be estimated from Equation 1 as $\Delta T/\Delta F$ and is closely similar to S' [1]; TCR can be calculated from observational data given estimates of ΔQ, ΔF, and ΔT. The temperature change associated with TCR will always be less than that for ECS, because the rate of temperature change responds to and lags the radiative forcing, due to thermal inertia [58]. A recent review [3] has suggested that scientists and policymakers shift attention from ECS to TCR, because TCR can be more precisely constrained by instrumental data and because its timescale is more relevant to decision-making.

Ice sheet and vegetation feedbacks are not included in standard definitions of ECS and TCR, because some of the relevant processes operate at timescales of centuries to millennia. Hence, **Earth System Sensitivity (ESS)** describes the sensitivity of Earth's global mean temperature to changes in radiative forcing when all fast and slow feedbacks in the Earth system are included [27]. Earth system models and proxy data for the Pliocene suggest that ESS is 30 to 50% greater than ECS [59].

2.2 Estimates of ECS and ESS from Earth System Models and Observations

The range of estimates for ECS remains large, despite decades of effort to refine them. The original Charney Report estimated an ECS of 1.5 to 4.5°C [2]. The 2013 Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report confirmed a likely range of 1.5 to 4.5°C, that ECS was extremely unlikely to be <1°C, and very unlikely to be >6°C [60]. The newest ESM experiments for CMIP6, however, suggest a higher ECS, with a newly reported range of 1.8 to 5.6°C across 28 ESMs and 10 ESMs reporting an ECS >4.5°C [57]. This apparently higher ECS is attributed to strengthened amplification by cloud feedbacks in the Southern Hemisphere [57,61]. These higher ECS are, however, higher than those estimated from observational data, which support an ECS between 1.5 and 4.5°C [3].

Most ESMs rely on general circulation models of the atmosphere and oceans (AOGCMs), in which ECS is an emergent outcome of the model simulations. However, some Earth system

models of intermediate complexity (EMICs) rely on a less detailed physics and add climate sensitivity as a parameter that can be adjusted to optimize model fit to observational data [e.g. 29]. Many kinds of observational data have been used to constrain estimates of ECS and TCR [1,4,62]. In general, 20th- and 21st-century instrumental data are best suited for estimating TCR and tend to produce lower estimates of climate sensitivity [ca. 1 to 3°C, 3], while paleoclimatic data are best suited for estimating ECS and ESS. The central tendency of ECS estimates from paleoclimatic data is 3°C, i.e. directly centered in the Charney range, but, depending on how uncertainties are modeled, paleoclimatic estimates for ECS range widely, from 1 to 5°C or from 0 to >6°C [3]. New proxy-based estimates of surface temperatures at the LGM are consistent with an ECS of 3.4 °C (95%CI: 2.4-4.5 °C) [6,7]. The new and high ECS estimates associated with CMIP6 models appear to be incompatible with Eocene climate reconstructions [61]. Hence, better constraining ECS is a central goal of climate change science and for paleoclimatology in particular (Section 4).

3. ECOCLIMATE SENSITIVITY: DEFINITION AND PRIOR USAGE

Here we propose a simple and flexible definition of **ecoclimate sensitivity ($\beta_{e,c}$)**: the amount of local ecological response per local climate change: $\beta_{e,c} = f(\Delta E_e/\Delta C_c)$. This definition is broad, because it allows for wide variation in both the ecological response variable and climate variable, and flexible, because it allows for both linear and non-linear $\Delta E/\Delta C$ responses. The *e* and *c* subscripts denote the choice of climate and ecological variables. One simple variant, **ecothermal sensitivity**, focuses on ecological responses per unit change in mean annual temperature $\beta_{e,\,TANN} = f(\Delta E/\Delta T_{ANN})$. We specify here mean annual temperature because it is widely measured across many systems and scales. However, alternative usages of ecothermal sensitivity might focus upon bioclimatic temperature dimensions such as growing degree days or extreme minima [63]. In this definition, the flexibility in choice of ecological response variable creates challenges of comparability among studies of ecoclimate sensitivity, yet is essential, because so many different ecological response variables are relevant. Further work may help to establish a classification and nomenclature of ecoclimate sensitivity for particular focal response variables. As we show in the rest of this section, this definition of ecoclimate sensitivity is consistent with most (although not all) prior usage, and some common focal response variables can already be identified, e.g. rates of tree growth, species range position, or community turnover.

The ecoclimate sensitivity literature is young and scattered, with so far no unified definition of ecoclimate sensitivity, despite wide and growing use (Fig. 1, Table S1). Because ecological systems respond to multiple abiotic and biotic factors, efforts to estimate climate sensitivity must disentangle multiple dimensions of climate change, other non-climatic factors, and ecosystem responses. Furthermore, because ecoclimate sensitivity varies within and across ecological systems [16,64], ecoclimate sensitivity research has not followed the atmospheric-sciences path of estimating a single global sensitivity value with uncertainty and instead focused on understanding the patterns and processes that govern variations in ecoclimate sensitivity across regions, time periods, ecological systems, ecological state variables, and metrics (Table S1). There has been no attempt yet to delineate different forms of ecoclimate sensitivity by timescale or included processes, as has been achieved for climate sensitivity. Given that most ecological studies have operated at temporal extents of decades to a century, arguably most

ecologists are analyzing a form of ecoclimate sensitivity that resembles the Transient Climate Response version of climate sensitivity (Section 2.1). Ecoclimate sensitivity is best developed in the dendroecological and conservation biology literature (Table S1, Fig. 2), but these fields employ very different approaches.

Written definitions of ecoclimate sensitivity mostly come from the climate-adaptation literature. Dawson et al. [65] and Glick et al. [66] defined the vulnerability of species and ecosystems to climate change as the product of three factors: climate exposure (magnitude of local climate change), sensitivity of the species or ecosystem to climate change, and the adaptive capacity of the species or ecosystem. Sensitivity was further defined as the 'degree to which the survival, persistence, fitness, performance, or regeneration of a species or population is dependent on the prevailing climate' [65]. Culp et al. [67] defined ecoclimate sensitivity as the physiological ability of a species to tolerate change. However, Beever et al [68] pointed out that in this standard three-part framework, an unclear distinction between 'sensitivity' and 'adaptive capacity' often led to underestimates of species adaptive capacity, because e.g. shifts in phenology, phenotype, and distribution are often all part of a suite of adaptive responses by species to changing environments, yet can also be indices of sensitivity. Hence, our working definition of ecoclimate sensitivity is narrower than that employed by [65,66], because it focuses on the measurable responses of ecological variables per unit local climate change, rather than ultimate outcomes such as survival, persistence, or adaptive capacity.

Our definition is closer to that used in papers attempting to quantitatively estimate ecoclimate sensitivity. These papers usually rely upon multivariate approaches, in which various climate predictors are analyzed jointly. Of the 126 papers reviewed, 105 analyzed more than one variable. Most papers (70) analyzed both temperature and hydrological variables (Fig. 2B, Table S1), with many variants of variables (e.g. growing degree days, minimum daily temperature, vapor pressure deficit) and spatiotemporal grains (Table S1). The most common analytical approach (Table S1) is some form of a linear model in which climate sensitivity is expressed as one or more coefficient(s) with an ecological response variable (such as tree growth rate or population abundance) expressed as a linear function of one or more climate predictors (Fig. 2C) [e.g. 64,69,70-72]. Other variants exist. For example, Seddon et al. [16] defined the Vegetation Sensitivity Index as the ratio of vegetation productivity to climate variance across multiple climate variables (monthly temperature, precipitation, cloud cover), weighted by their ecological importance [16]. Culp et al. [67] developed a five-point ordinal scale for rating ecoclimate sensitivity, while Rudgers et al. [23] defined climate sensitivity functions as a flexible but univariate framework to handle non-linear relationships between precipitation and net primary productivity. In paleoecology and community ecology, dissimilarity metrics are commonly used to summarize multi-species responses to environmental forcing, and have been used to explore ecological sensitivity at the community level [73]. In economics, Riccardian climate analyses regress economic variables against climate and other variables [e.g. 74], and so are a form of [eco]climate sensitivity analysis.

Ecoclimate sensitivity is well developed in forest ecology, where permanent forest plots and long time-series of ring widths support estimates of ecoclimate sensitivity at an annual temporal grain for tree growth rates and associated variables such as forest composition and carbon sequestration. Of the 126 ecoclimate papers analyzed here, nearly half (53) were from the dendroecological literature (Fig. 2A). Charney et al. [69] modeled climate sensitivity with tree

growth rates as a linear function of monthly temperature and precipitation, and growth-climate sensitivity allowed to vary among 13 life zones in North America. Sullivan et al. [75] analyzed 590 permanent forest plots across the tropics and found that forest biomass was most sensitive to temperature of the warmest month, with a thermal sensitivity of forest biomass of -9.1 MgC ha^{-1} $°C^{-1}$. A data–model comparison indicated that terrestrial ecosystem models under-predicted the thermal sensitivity of tree growth and over-predicted sensitivity variability over the last 30 years [76]. Ols et al. [77] reported that apparent changes in tree-growth climate sensitivity in eastern boreal North America could be traced to uncertainties in the climate data and a sparse meteorological network. In Amazonian rainforests, carbon sequestration and tree demography exhibit a higher climate sensitivity in secondary forests than primary forests [78]. Similarly, in the boreal-temperate forests of eastern North America, the ecoclimate sensitivity of carbon sequestration and forest biomass was higher in young forests than old forests [13].

In conservation biology, efforts have focused on identifying climate-sensitive species. Early papers relied upon expert elicitation to identify climate-sensitive species [79], while Mims et al. [80] used spatial occurrence data cross-referenced with climate variables to estimate environmental niche breadth and use it as an indicator of climate sensitivity. If the Dawson et al. [65] framework is used, some earlier papers reported as climate-sensitivity analyses are actually climate-vulnerability analyses, because these papers rely upon species distribution models and future climate projections (i.e. climate exposure) to estimate the effect of climate change on a species [e.g. 81,82].

In other studies, Amburgey et al. [20] tested the hypothesis that range-margin populations were more sensitive to climate fluctuations than range center populations, using wood frogs, and found no clear support for this hypothesis. Similarly, Jarema et al. [83] found that beaver abundances were more sensitive to climate in areas of high abundance and less sensitive at range margins. Note too the long and broad tradition of studying the relationship between environmental and ecological variables [e.g. 84]; many relevant papers aren't captured by a simple search for 'climate sensitivity' (Figure 1).

4. CLIMATE & ECOCLIMATE SENSITIVITY AT THE LGM: CONSTRAINTS AND INHERENT TRADEOFFS

4.1 LGM and Proxy Constraints on Climate Sensitivity

For decades, the LGM has been a focal period for assessing climate sensitivity [28,30,85,86], for several reasons. First, the radiative forcing by increased ice-sheet extent and lower greenhouse gas (CO_2, CH_4, N_2O) concentrations was large, with greenhouse gas forcings well constrained by ice cores [31], while the orbital forcing was similar to present [87]. The absolute increase in $[CO_2]_{atm}$ concentrations from the LGM to pre-Industrial time period (187 to 280ppm, +93ppm) is smaller than the increase from the start of the Industrial Revolution to present (280 to ca. 415ppm and rising, +135ppm), but the two are nearly equal in relative terms (+50% vs. +48%). Hence, because of the log-linear relationship between atmospheric greenhouse gas concentrations and radiative forcing (Section 2.1), the two are nearly equal in their magnitude of radiative forcing. The total radiative forcing from CO_2, CH_4, and N_2O from 1750 to 2011 CE is +2.82 W m^{-2} [88], while the negative forcing for these greenhouse gases at the LGM relative to

pre-Industrial is -2.8 W m^{-2} [89]. At the LGM, this reduced greenhouse gas forcing was amplified by increased surface albedo, due to increases in ice and snow extent and increased land area exposed by lowered sea levels, giving a total shortwave albedo forcing of -2.6 to -3.5 W m^{-2} [90]. Changes in radiative forcing due to increased atmospheric aerosol loadings and changed vegetation cover are likely important but poorly constrained [31].

Second, because of the long duration of the last glacial period (70 to 100ka, depending on which Marine Isotopic Stages are included) and the slow cooling that preceded the LGM, Earth surface temperatures can be assumed to be in quasi-equilibrium with radiative forcing during the LGM, making it suitable for shorter 'snapshot' simulations with ESMs, in which the radiative forcings and other boundary conditions are set and ESMs run to equilibrium. This assumption of equilibrium is a convenient and reasonable simplification, but is violated in detail in the real world given e.g. abrupt millennial-scale climate events [91].

Third, dense networks of paleoclimatic proxy records are available to constrain global surface temperature at the LGM and other time periods (Fig. 3). The paleoclimatic syntheses for the LGM and other time periods rely on a combination of biological, geochemical, and physical indicators of past climates (Fig. 3). Biological indicators can be further divided into community-based proxies (in which climate variables are inferred from past changes in the abundance of climate-sensitive species), individual-based proxies (past climates inferred from changes in growth rates or other physiological signals from individual organisms), or biogeochemical (based on the changing proportion or isotopic fractionation of organic compounds) (Fig. 3). Specific compilations for the LGM include MARGO [92], Tierney et al. [6], and Osman et al. [93] for sea surface temperatures, Bartlein et al. [33] for terrestrial surface temperature reconstructions at the LGM, and the Shakun et al. [94] compilation of ice cores and other time series from the LGM to present. These paleoclimatic proxy syntheses have relied heavily on biological indicators (community, individual, biogeochemical), with the average proportion of biological proxies at 73% and ranging from 22 to 100% (Fig. 3).

Establishing exactly how cold the LGM was, and by extension Earth's climate sensitivity, is a long-standing question in paleoclimatology. The CLIMAP project [95] used paleoclimatic transfer functions applied to marine micropaleontological assemblages to estimate a global average sea-surface temperature (SST) reduction of 2.3°C and no temperature change in subtropical oceans. The MARGO update to CLIMAP used 696 biological and geochemical records and reported a global decrease in SSTs of 1.9°C at the LGM, with the largest cooling in the northern Atlantic (10°C), the Southern Ocean, and tropical Atlantic [92]. These mild estimates of LGM cooling were contraindicated by terrestrial montane changes in snowline and equilibrium line elevation, which suggested LGM cooling on the order of 3.9 to 5.5°C [96]. Pollen-based syntheses indicate similar or larger terrestrial LGM cooling, reaching 3°C in the tropics and over 8°C near the Northern Hemisphere ice sheets [33]. Hansen et al. [97] used the CLIMAP boundary conditions and an early version of the NASA-GISS GCM to estimate an ECS of 2.5 to 5°C. The first round of simulations by the Paleoclimatic Modeling Intercomparison Project (PMIP1) reported a global mean cooling of 4°C for atmosphere-only GCMs [98], while for PMIP2, reported LGM cooling is 3.6 to 5.7°C [89].

Recent efforts have focused on assimilating paleoclimatic proxy networks with ESM simulations, to better constrain global mean temperature changes and ECS [6 ,28-30,85,99].

Initial efforts with EMICs tended to simulate higher LGM cooling and ECS, with e.g. a simulated LGM cooling of 4.4 to 7.2°C by the CLIMBER-2 EMIC [100] and a LGM cooling at 5.3 to 7.5°C simulated by the GENIE-2 EMIC, with a corresponding ECS of 2.6 to 4.4°C. In contrast, the UVic EMIC estimated a climate sensitivity of 2.3°C with a 66% CI of 1.7 to 2.6°C, much lower and narrower than the Charney and IPPC range [29]. The UVic simulations were constrained by the MARGO marine and Bartlein et al. terrestrial reconstructions, with the marine reconstructions providing a stronger influence on the posterior estimate. Annan and Hargreaves [28,30] combined prior proxy syntheses with the PMIP2 AOGCM simulations, using a pattern-scaling approach in which the temperature anomaly fields for each model were adjusted by a scalar factor to maximize the fit between model-simulated and proxy-reconstructed temperature anomalies. This approach produced a global surface cooling of 4°C (95 CI: 3.2 to 4.8°C) at the LGM and a ECS of 2.5°C, with a better statistical model-data fit than reported for the UVic EMIC data–model assimilation [28,30]. In a new major effort, Tierney et al. [6] assimilated a proxy network of 955 marine organic and inorganic geochemical reconstructions of SSTs (Fig. 3) with a 40-member ensemble of the isotope-enabled Community Earth System Model. They report a global mean temperature change of 6.1°C (95% CI: 5.7 to 6.5°C), and a resultant ECS of 3.4°C (95% CI: 2.4 to 4.5°C) [6]. (A follow-on paper by Osman et al. [93] increased the estimated global mean temperature change to 7.0°C +-1.0°C [2σ].) Note that the estimated surface air temperature change is greater than the estimated ECS because of additional negative radiative effects on the Earth System due to expanded ice sheets and increased atmospheric aerosol loadings that are not included in ECS (Section 2).

4.2 Ecoclimate Sensitivity at the LGM

The sensitivity of species and ecosystems to the transition from colder and generally drier climates of the LGM to the present is clear and unambiguous, with legacies that persist today, yet ecoclimate sensitivity remains poorly quantified. Micropaleontological time-series of community composition that span one or more glacial-interglacial cycles show large variations that match ice-core records of greenhouse gas composition and global ice volume, with this close coupling observed across terrestrial and marine records and across latitudes [101-105]. In middle and upper latitudes, thermophilous species contracted their ranges into glacial refugia, from which they expanded during post-glacial temperature rises [38,106,107] (Fig. 4A,B). In tropical montane regions, both individual species' ranges and treelines shifted downslope at the glacial period by 1,000 to 1,700 meters [108-110], although some locations show high ecosystem stability [111]. Most regions experienced large rates of compositional turnover between the LGM and present (Fig. 4C). Terrestrial biomes of the LGM were characterized by more open conditions and lower tree cover (Fig. 4D), with the carbon sequestration of LGM terrestrial reservoirs reduced by roughly 600 Gt C relative to the pre-Industrial period [112-114].

Contemporary patterns of biological diversity and distributions still carry detectable legacies of the last glacial period. In Europe, contemporary distributions of species richness for plants and animals are partially predicted by climate stability since the LGM, with higher richness in regions that are more climatically stable and with fewer barriers to dispersal [115,116]. Globally, distributions of small-ranged endemic species are concentrated in regions of low post-glacial climate velocity [44]. Within species, the fragmentation of populations into

genetically isolated refugia, followed by limited genetic mixing during postglacial range expansion, means that many contemporary populations have distinct genetic signatures that can be traced to their glacial refugial populations [117-119].

Because of the clear and profound ecological effects of the LGM and earlier glacial-interglacial cycles, paleoclimatologists, paleoecologists, and phylogeographers have all employed ecoclimate sensitivity as a foundational tenet, and from this common foundation have advanced in different directions. Paleoclimatologists often use paleoecological data, in combination with statistical models that invert ecological response functions to infer past climates from the fossil abundances of organisms [120,121], to estimate past temperatures and use these paleotemperature reconstructions to estimate climate sensitivity (Fig. 3, Section 4.1). Concurrently, paleoecologists, macroecologists, and phylogeographers have sought to understand how the past and present distribution and diversity of species was shaped by the interactions between climate-driven ecological dynamics and other factors such as varying $[CO_2]_{atm}$, potential trophic effects associated with the late-Quaternary megafaunal extinctions, altered fire regimes, and the worldwide growth and spread of human populations. Much of the recent paleoecological and biogeographic literature has focused on ecological dynamics during the post-LGM warming, to gain insight into biodiversity responses to anthropogenic climate change [42].

However, ecoclimate sensitivity itself remains understudied and poorly quantified in paleoecological records. A rare exception is Nolan et al. [35], who estimated the climate sensitivity of terrestrial ecosystems based upon a qualitative expert classification of 594 fossil pollen records as having large, moderate, or low vegetation changes (Fig. 4C). Here, ecoclimate sensitivity is measured as the probability of a large compositional or structural change as a function of temperature, with e.g. a ca. 70% probability of a large compositional change with 4ºC warming. Other studies have used paleoecological records to assess ecoclimate sensitivity to post-LGM climate variations. Seddon et al. [73] reported an overall linear response of vegetation changes in northern Europe to the large deglacial changes in North Atlantic temperature, while the same model fitted for the Holocene records showed no overall relationship with temperature. This apparent temporal change in sensitivity may indicate that local vegetation changes and complex site-level responses are masking regional-scale ecological responses to smaller climate changes. Many papers have assessed ecoclimate sensitivity in qualitative terms. For example, Rull et al. [122] compared a series of biodiversity indices to independently reconstructed temperature and moisture changes in high- and mid-elevation Andean sites from Venezuela across the Younger Dryas. They noted only 10-15% of recorded pollen types as being classified as sensitive to warming in their sites, with sensitivity defined at by qualitatively identifying those pollen taxa that showed the greatest amount of the variation in each record. Morel and Nogue [123] explored whether satellite-based and pollen-based indicators of late-Holocene vegetation sensitivity were congruent.

These few studies just scratch the surface, however, and in general ecoclimate sensitivity remains poorly constrained for pre-instrumental time periods (Table S1, Fig. 2E). Given that biodiversity trends are known to be sensitive to choice of response variable and spatiotemporal scale [43], a key research need is to understand how ecoclimate sensitivity varies across biodiversity variables, systems, and at scales ranging from local to global. This effort can be

powered by the increasing precision of paleoclimatic reconstructions [6] and by the growing availability of networks of paleoclimatic and paleoecological data [32,124,125].

4.3 A Joint Consideration of Climate and Ecoclimate Sensitivity: Tradeoffs and Implications

Several points emerge from the above review. First, paleoclimatic data offer a major constraint on the climate sensitivity of the Earth system, and within this the LGM is perhaps the single most important period for estimating equilibrium climate sensitivity, given the strength of forcing and density of proxies. Estimates of ECS have continued to narrow, as proxy networks and Earth system models are enhanced and assimilated [86]. Within these paleoclimatic studies, paleoecological and paleobiological data (and their underlying assumptions of ecoclimate sensitivity) provide a large and under-appreciated constraint on ECS, given that paleo-community and biogeochemical data are the backbone of many paleoclimatic reconstructions, ranging from 22% to 100% of proxy records for the LGM and other time periods (Fig. 3).

Second, macroecologists and paleoecologists must use the next generation of paleoclimatic reconstructions with caution, because of the growing trend to assimilate information from both ESMs and proxy networks. From the perspective of a paleoclimatologist seeking to constrain climate sensitivity, there is a strong rationale for employing all relevant kinds of proxy data (physical, chemical, biological, historical) and assimilating them with Earth System models. However, the obvious danger here from a paleoecologist's perspective is circularity: if proxy networks that are assimilated with the ESMs include paleobiological data, then any resultant temperature inferences cannot be used to study the ecoclimate sensitivity of the same organisms. For example, the ECS estimates by Schmittner et al. [29] are primarily constrained by the fossil pollen networks and marine microfossil assemblages, and so cannot be used to study vegetation responses to LGM climates. The new compilations by Tierney et al. [6] are promising for terrestrial biogeographers, because they rely only on marine geochemical proxy networks. Hence, this paleoclimatic assimilation product does carry embedded some biological influence, with respect to the ecoclimate sensitivity of organic biomarkers, but the contribution is modest and confined to marine records, so there should be little or no circularity when using these marine-based temperature assimilation products to study the past ecoclimate sensitivity of terrestrial ecosystems.

Third, and perhaps most interestingly for global change biologists who use the past to study the ecological impacts of changing climates, this joint review reveals a tradeoff between past estimates of climate and ecoclimate sensitivity. Given that $[CO_2]_{atm}$ variations over the last 800,000 years are known precisely, estimates of climate and ecoclimate sensitivity must be inversely proportional to each other. If the lower-end estimates of post-LGM warming and ECS are correct [e.g. ΔLGM=2.2°C, ECS = 2.3°C, 29], then ecoclimate sensitivity must be very high, i.e. a small global warming since the LGM profoundly transformed biological systems (Fig. 4). For example, this small global warming and the associated $[CO_2]_{atm}$ changes would have triggered moderate to large impacts on both composition and structure for over 95% of terrestrial vegetation [35]. Conversely, if the upper-end estimates of post-LGM warming and ECS are correct [e.g. Δ LGM=5.9°C, ECS=3.2°C, 6], then the ecoclimate sensitivity to these temperature changes must be more muted. From this biospheric perspective, the intense attention that climate

sensitivity has received in the public and scientific literature is understandable, but the issue is also somewhat moot. Given the large ecosystem transformations from the LGM to present, either climate sensitivity must be high or ecoclimate sensitivity must be high, but regardless we can expect large biospheric responses to the roughly 135 ppm (and rising) increase in $[CO_2]_{atm}$ since the pre-Industrial period.

Fourth, from the perspective of understanding the biospheric impacts of past and future climate change, a key need is to constrain more tightly both climate and ecoclimate sensitivity and understand the processes governing their variations across space and time. Because high uncertainty in climate sensitivity translates to high uncertainty in ecoclimate sensitivity (for the last 800,000 years, when $[CO_2]_{atm}$ variations are known precisely but temperature is not), reducing uncertainty in estimates of climate sensitivity also reduces uncertainty in ecoclimate sensitivity. Hence, more narrowed estimates of LGM cooling, e.g. the 95% CI ranges of 5.6 to 6.3°C for LGM cooling reported by Tierney et al. [6], are valuable not just because they better constrain ECS, but also because they support more precise estimates of ecoclimate sensitivity.

Fifth, this review reveals an important imbalance between the paleoclimatic and paleoecological literatures on climate and ecoclimate sensitivity at the LGM. One field has justly devoted enormous attention to estimating climate sensitivity, while the other has barely attended to ecoclimate sensitivity. Yet arguably, from an impacts perspective, the latter matters far more. We are now in a world in which we see the ecological impacts of climate change emerging all around us, ranging from the ongoing shifts in species' distributions [55,126], to the intensified droughts and fires in semi-arid regions such as Australia and the western US [127,128], to the collapses of coral populations [129]. Quantifying and predicting ecoclimate sensitivity, its intersection with other global change drivers such as land use and species extinctions, and the factors that cause ecoclimate sensitivity to vary across space, time, and ecological systems, is one of the most pressing challenges of our time.

5. ECOCARBON SENSITIVITY: SCALING FROM GLOBAL $[CO_2]_{atm}$ VARIATIONS TO LOCAL ECOLOGICAL RESPONSES

A challenge apparent from the above synthesis is the scale mismatch between climate and ecoclimate sensitivity: one global, the other usually local to regional. This scale mismatch is perhaps the biggest practical barrier to integrative studies of climate and ecoclimate sensitivity. This mismatch is particularly important for pre-instrumental time periods, because of the tradeoff between estimates of climate and ecoclimate sensitivity, but the problem is general. Here, we present a simple theoretical framework for combining climate and ecoclimate sensitivities, along with a climate scaling term, to assess the sensitivity of local ecological systems to changes in greenhouse gas concentrations, which we call here **ecocarbon sensitivity** ($\boldsymbol{E_{CO_2}}$):

$$E_{CO_2} = S' * A_c * \beta_{e,c} \qquad \text{(Eq. 2)}$$

Here $\boldsymbol{E_{CO_2}}$ expresses the local ecological response as a function of a change in global $[CO_2]_{atm}$, or, more precisely, the change in radiative forcing caused by a change in $[CO_2]_{atm}$. S' is the climate sensitivity factor (Section 2) with units of °C $(W\ m^{-2})^{-1}$, A_c is a scaling factor that expresses the sensitivity of the climate variable(s) of interest to global mean surface temperature

[6,130], and $\beta_{e,c}$ is ecoclimate sensitivity ($f(\Delta E/\Delta C)$; Section 3). This definition focuses on the responses of ecological systems to local climate changes, so direct physiological effects of changing $[CO_2]_{atm}$ upon organisms are not explicitly considered in this formulation [112,131]. This formulation of ecocarbon sensitivity carries similarities to the Vegetation Sensitivity Approximation (VSA) of Claesson and Nyctander [132], which established a model for plant productivity in semi-arid systems as a function of $[CO_2]_{atm}$, temperature, and precipitation, in which temperature was expressed as a logarithmic function of $[CO_2]_{atm}$.

This formulation implies that ecocarbon sensitivity often will be logarithmic, because of the logarithmic sensitivity of global mean temperature to $[CO_2]_{atm}$ (Section 2). The scaling factor *A* is uncommon in ecology but often employed in climatology to calculate, e.g., scaling factors of sea surface temperatures to global mean surface temperatures [6,130] or local projected surface temperature and precipitation changes to 21st-century projections of global mean surface temperature [4, Fig. 12.10]. $\beta_{e,c}$ can take many forms and will vary by spatiotemporal scale, response variable, and ecological system (Section 3). At a fundamental level, most ecological responses to temperature have a unimodal form, with minimum and maximum thermal limits to organismal survival and biological processes. However, at local to regional scales ecological responses, such as variations in vegetation productivity [16] or variations in tree or shrub growth rates [69,133,134] (Table S1), can often be treated as linear responses to changes in temperature [135]. Other common response forms include unimodal distributions of species abundances along environmental gradients [84] or non-linear, hysteretic responses with alternate stable states [136], but these types of response functions are rarely explicitly represented in the ecoclimate sensitivity literature [but see 137].

CONCLUSIONS

At present, 'climate sensitivity' is used simultaneously by different global-change disciplines to describe at least two very different things: sensitivity of global mean temperatures to atmospheric CO_2 concentrations and sensitivity of ecological systems to changes in climate. When assessing climate and ecoclimate sensitivity jointly, several important points emerge. First, the use of the same term for fundamentally different things leads to confusion, so we recommend renaming the later ecological usage. Second, the two concepts have been studied very differently, with the atmospheric sciences employing more formal definitions and treating climate sensitivity as a global parameter to be better constrained, while usage in the ecoclimate literature employs a multivariate framework and an emphasis on assessing the processes governing the variations in ecoclimate sensitivity across spatiotemporal scales and systems. Third, past time periods such as the LGM have been closely studied to reduce uncertainty in estimated climate sensitivity, yet ecoclimate sensitivity remains underexplored and poorly quantified. There is also risk of circularity, if the same paleoecological proxies are used in both paleoclimatic and paleoecological assimilation products. Fourth, given that $[CO_2]_{atm}$ is well constrained for the last 800,000 years, this joint consideration reveals an inherent inverse relationship between climate sensitivity and ecoclimate sensitivity: higher estimates of climate sensitivity for the LGM (and other past time periods) imply a lower ecoclimate sensitivity, and vice versa. Either way, the profound biospheric transformations associated with the transition

from the LGM to the Holocene suggest similarly large biospheric changes over the coming decades. This conclusion is insensitive to estimates of climate sensitivity. Fifth, in a simple theoretical framework, climate and ecoclimate sensitivity can be combined with a global-to-local climate scaling term to calculate ecocarbon sensitivity, i.e. the sensitivity of local ecosystems to the radiative forcing caused by global changes in $[CO_2]_{atm}$. Sixth, given this framework, ecocarbon sensitivity is often expected to scale logarithmically to $[CO_2]_{atm}$, because of the logarithmic response of global mean surface temperatures to $[CO_2]_{atm}$. Better constraining ecoclimate sensitivity, and the processes determining its variation at local to global scales, is a critical need for the future, powered in part by increasingly precise paleoestimates of climate and ecoclimate sensitivity.

FIGURES

Fig. 1 Number of papers focusing on climate sensitivity in the atmospheric and meteorological sciences (blue line) or in ecology and biodiversity conservation (orange line). Search based on a Web of Science search for ((Title: ”climate sensitivity”) OR (Topic: “climate sensitivity”)) on June 23, 2020 for all years through 2019. In the atmospheric sciences, the first discovered use is in 1978 with a peak in 2018 of 94 papers. In ecology and conservation biology, the first discovered use is in 1993 with a peak in 2019 of 26 papers.

Fig. 2 Meta-analysis of papers from the ecoclimate literature (Table S1). A) Ecoclimate papers categorized by their focal taxa or ecosystem type. B) Combinations of climate variables analyzed in the ecoclimate sensitivity literature. ‘Indices’ refers to climate indices such as the Southern Ocean Index or the Pacific Decadal Oscillation. C) Analytical Method employed, broadly organized into methods employing linear models, process-based models (PBMs), species distribution models or community-level models (SDMs/CLMs), or other. D) Papers categorized by the primary domain used to assess climate sensitivity: studies in which the primary analysis focused on temporal variations in climate and ecological system response, spatial variations, both, or studies in which experimental manipulations were used to establish contrasting climatic conditions. E) Temporal extent of studies.

Fig. 3 Paleotemperature proxy syntheses for the LGM and other time periods of interest to Earth system modelers (Pliocene, Holocene, Late Holocene), in which the proxies are categorized by type: 1) Community assemblages, in which past temperatures are inferred based on the ecoclimate sensitivity in community composition of temperature-sensitive taxa such as diatoms, dinoflagellates, foraminifera, ostracodes, and plants (pollen); 2) Tree Growth, in which past temperatures are inferred based on the ecoclimate sensitivity of ring width, ring density, and other indices of tree growth rates; 3) Organic Geochemical (BGC), in which past temperatures are inferred based on the ecoclimate sensitivity of the microbial production rate of specific organic compounds; 4) Inorganic Geochemical (GC), primarily stable isotopes, and 5) Other. Categories 1-3 all rely on ecoclimate sensitivity, at levels ranging from physiological processes within individual organisms to communities. Among the major paleoclimatic proxy syntheses shown here, the proportion of ecoclimate proxies ranges from 22% to 100%, with an interstudy average of 73%.

Fig. 4 Effects of LGM climates on vegetation. Panels A & B show changes in *Picea* (spruce) and *Quercus* (oak) distributions between the LGM and late Holocene, based upon fossil pollen percentages from the Neotoma Paleoecology Database. Darker dots indicate sites where these taxa were reported at the LGM (23 to 19 ka), while lighter dots indicating presence during the late Holocene (2 to 1 ka). For *Picea*, an abundance threshold of 3% was used, while, for Quercus, 3% was used. Panel C is a sensitivity function for the LGM, showing the probability of large compositional or structural changes in vegetation as function of local temperature change, from [35]. Panel D shows inferred biome distributions at the Last Glacial Maximum, replotted from [112].

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