Opinion

Using Climatic Credits to Pay the Climatic Debt

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Many organisms are accumulating climatic debt as they respond more slowly than expected to rising global temperatures, leading to disequilibrium of species diversity with contemporary climate. The resulting transient dynamics are complex and may cause overoptimistic biodiversity assessments. We propose a simple budget framework to integrate climatic debt with two classes of intervention: (i) climatic credits that pay some of the debt, reducing the overall biological change required to reach a new equilibrium; and (ii) options to adjust the debt repayment rate, either making a system more responsive by increasing the rate or temporarily reducing the rate to buy more time for local adaptation and credit implementation. We illustrate how this budget can be created and highlight limitations and challenges.

Highlights

Many taxa respond relatively slowly to rising global temperatures, resulting in a disequilibrium between observed and expected biodiversity known as the 'climatic debt'.

Recent empirical work has demonstrated how local-scale climate adaptation options can be conceptualised as climatic credits that pay part of the debt.

Other adaptation options focus on adjusting the rate at which debt is repaid (allowing equilibrium to be restored), attempting to make ecosystems more or less responsive to climatic change.

A climatic budget can be assembled by uniting climatic debt with options to supply credit and alter the repayment rate, providing a simple way to capture transient dynamics and communicate different management scenarios.

Climatic Debt and Credit and the Value of Budgeting

In response to climate change, organisms must migrate, adapt via phenotypic or evolutionary mechanisms, or face extinction [1]. Across many parts of the world and a range of taxa, changes in species' distributions following recent decades of climate change have been smaller than expected. The difference between observed and expected changes is described as **climatic debt** (see Glossary) (Figure 1), which is 'repaid' when biodiversity reaches equilibrium with the new climate. The prime focus of such analyses has been rising temperatures. Recent studies suggest that climatic debt in contemporary plant and animal assemblages could be equivalent to ~0.4–1.3°C of warming or more (e.g., [2–9]) and there is widespread evidence for postglacial climatic debts in plant communities [10]. For some species, other dimensions of climate, such as precipitation, could be more important than temperature [11] or seasonal maxima could be key [9]. For simplicity, we focus on average temperatures, but climatic debt could equally be quantified in other units (e.g., mm precipitation year^{-1} [7]).

Climatic debts can be generated by limits to the rates of dispersal and establishment of more thermophilic species, by the slow loss of cooler-climate species [12] or by relatively slow changes in abundance among species that persist with increasing temperatures. The total debt may be influenced by numerous factors, including species' traits and landscape properties [5], which vary across spatial and temporal scales, and levels of biological organisation [13]. Although some taxa appear able to keep pace with temperature changes (e.g., [14]), the frequency of climatic debts suggests that many do not, which will lead to underestimates of climate change impacts and overly optimistic conservation assessments.

Set against the debt is a range of local or regional scale strategies that may be able to lower temperatures (e.g., by manipulating vegetation structure to increase shading) or reduce temperature impacts without cooling the system, such as the reduction of co-occurring stressors; comparable manipulations are possible for moisture-based debt [15]. Small-scale actions of this type can offset substantial temperature increases (e.g., 0.8–1.0°C [8,16]) and are more easily and rapidly achieved than globally coordinated climate action [17]. These interventions could be conceptualised as **climatic credits** to help pay the debt [8] (Figure 1). In the long-term, rising temperatures are likely to exceed the credits, but they should still reduce the overall magnitude

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and rate of biodiversity changes and the risk of catastrophic changes, such as ecosystem collapse [18].

Inspired by Jackson and Sax's [19] 'biodiversity budget', in which **extinction debt** is balanced against immigration credit, we outline a framework uniting climatic debts, credits, and factors that could affect the **repayment rate** (Figure 1). Although a climatic budget is a greatly simplified view of the manifold influences on species distributions, it would be valuable for communicating with practitioners, conservation organisations, policy makers, and other stakeholders including the general public [19]. The forecasts from climate models are familiar to these groups, with time series of predicted temperature increases and maps of future climate regularly appearing in the media. Climatic debts and credits could be mapped directly onto these predictions, using the same units, to allow simple comparisons of environmental change, biodiversity responses, and the extent to which management interventions may be able to offset the impacts. Budgeting is readily understood and applied by a wide range of stakeholders, and long-term conservation goals can be set in terms of minimising the debt. Furthermore, such budgets are explicit about time lags in biodiversity responses to global change – losses, gains, and turnover – that are vital to understand ecological responses [20–22]. However, these lags are challenging to quantify and communicate in simple terms and are frequently overlooked, leading to biased assessments of biodiversity.

Estimating Climatic Debts and Credits

Estimation of climatic debt begins with the quantification of the relationship between community structure and temperature, so that temperature can be inferred from the observed species composition (Figures 1 and 2). The most common approach is to calculate the **community temperature index (CTI)** from the **species temperature indices (STIs)** of the species present (e.g., [3,6,7,23,24]). To calculate the current climatic debt, the **inferred temperature** (e.g., CTI) is subtracted from the observed environmental temperature [2] (Figures 1 and 2); this is analogous to the difference between the observed and expected species richness for extinction debt [25]. Indebted communities have a greater frequency or abundance of cooler-climate species than expected, leading to an inferred temperature that is below the observed temperature (Figure 1). The calculation of a future climatic debt follows the same process, using predicted climate and community structure (Figure 2).

Estimating climatic debt is simple in principle, but it involves at least three important methodological challenges. The first is to obtain reliable estimates of temperature preferences based on distribution data, which is the familiar problem of trying to estimate aspects of the fundamental niche from the realised niche. Climate change is likely to generate novel communities and novel species interactions, leading to changes in the apparent relationships between temperature and species occurrence [26]. Possible solutions here include the augmentation or corroboration of distribution data with experimental data [26,27] and modelling of climate preferences without assuming equilibrium (see below). An added complication is the risk of climatic debt in the data used to calibrate the relationships [28]; this challenge can be reduced by using historical distribution data from prior to the rapid climatic changes of recent decades (e.g., [2]). Finally, phenotypic plasticity and rapid evolutionary change might write off part of the climatic debt (e.g., [5,12,29–32]), further complicating debt assessment and forecasting.

The second challenge is to develop realistic nonequilibrium models to predict species distributions and community structure. Disequilibrium can distort the predictions of traditional climate envelope models [33], which use simple species associations to describe the climatic niche and assume equilibrium. Such models will often fail to identify potential climatic debts. The

Glossary

Climatic credit: a change in the environment that offsets part or all of a climatic debt and can be quantified in the same units as the debt (e.g., °C or mm year^{-1}). Typically relates to management interventions that could reduce the debt.

Climatic debt: usually defined as the difference between the observed environmental temperature and the temperature at which the observed community would be at equilibrium with the environment (see 'inferred temperature'), in degrees Celsius; equally applicable to other environmental variables, such as annual precipitation.

Community temperature index (CTI): the average STI of the species present in a community, reflecting the mix of warmer- or cooler-climate species.

Extinction debt: the number of species predicted to become extinct in the process of a community reaching a new equilibrium with the environment. Habitat loss is the primary focus of most extinction debt studies, but climate may also contribute.

Inferred temperature: the predicted environmental temperature based on the assemblage of species present (e.g., by calculating the CTI); where a climatic debt is present, the inferred temperature will be lower than the observed temperature; also known as the reconstructed temperature.

Low-regrets interventions: management interventions that involve little risk of undesirable consequences and are likely to confer wider benefits on biodiversity or ecosystem service provision.

Process-based models: mechanistic models of community structure that incorporate aspects of colonisation, population growth, species interactions, and extinction. Such models can make predictions under both equilibrium and nonequilibrium conditions.

Relaxation time: the time taken for a system to reach equilibrium with current environmental conditions.

Repayment rate: the amount of climatic debt that can be paid off per unit time (e.g., °C year^{-1}); the inverse of the relaxation time.

Resistance: the extent to which a community changes in response to a perturbation. Highly resistant communities show little or no change to a disturbance.

Species temperature index (STI): the average temperature experienced by a species across its range; can be calculated from presence–absence or abundance data.

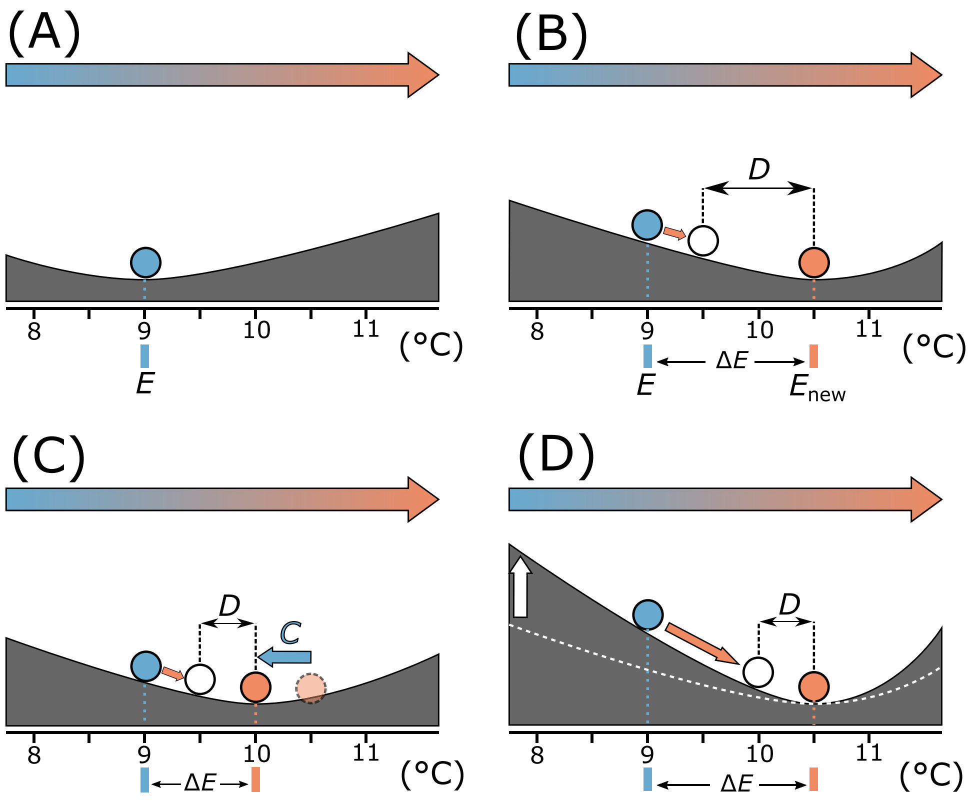

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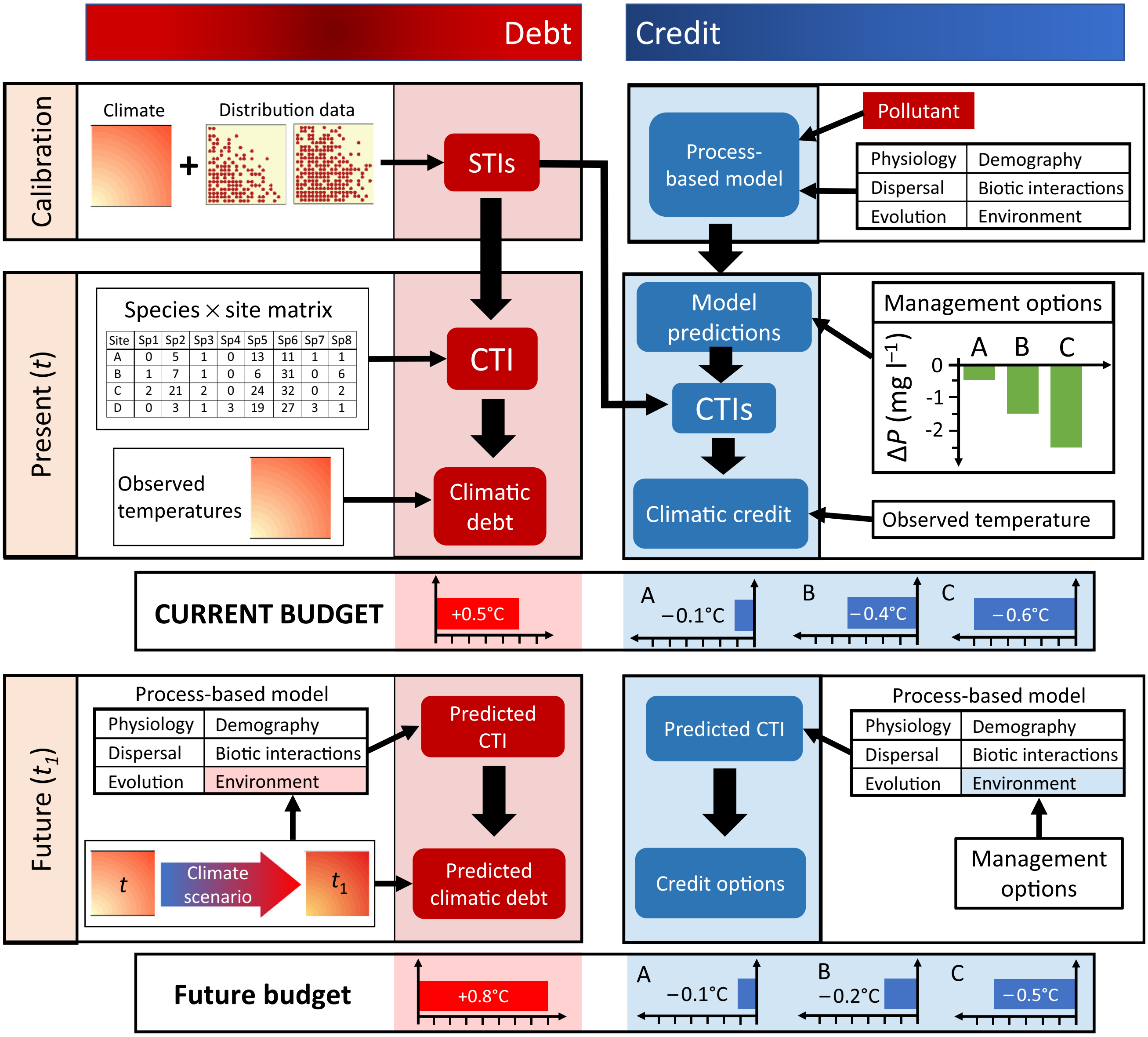
Figure 1. Basic Principles of Climatic Debt and Credit and Repayment Rate, Using the Familiar Ball-in-Landscape Analogy. Equilibrium community composition changes across the x-axis, with the relative abundance of species favouring warm temperatures increasing from left to right. (A) The system is at equilibrium (*E*) prior to climate warming, with the blue ball sitting at the bottom of the valley. (B) 1.5°C of warming changes the landscape, shifting the equilibrium point to the right (E_{new}; red ball): Δ*E* represents the biological change between *E* and E_{new}. The community (white ball) responds to the change, moving to the right, but at the time of observation has moved only part of the way towards E_{new}: the distance by which it falls short is the climatic debt (*D*), which is equal to 1°C here. (C) Climatic credit (*C*) offsets 0.5°C of the warming (e.g., via improved water quality), reducing Δ*E* and *D* to 1.0°C and 0.5°C, respectively, and increasing the community's resistance. (D) Measures to alter the repayment rate change the steepness of the valley sides. In this example, increased habitat connectivity creates a steeper-sided basin (broken white line = original basin shape), reducing relaxation times; although Δ*E* is 1.5°C as in (B), *D* is only 0.5°C.

solution is to adopt more mechanistic models that incorporate the biological processes generating the debt, such as dispersal, demographics, and biotic interactions (e.g., [12,34–36]). The development of such models represents a major challenge, but rapid progress is being made. Some researchers have extended conventional species distribution models to incorporate mechanisms such as dispersal and then 'stacked' individual species' predictions to estimate community structure. More recently, full **process-based models** have been used to generate forecasts [37–39]. The challenge for the implementation of these models is to control model complexity and obtain data to estimate process-based parameters [33]. Expansion of species-level phylogenies and databases of ecological traits may help to interpolate missing demographic data [38].

The third challenge is to quantify and reduce uncertainty in estimates of temperature preferences and community responses to climate change. Uncertainty may be introduced at numerous points, from limitations in species distribution data and uncertainty around climate forecasts,



Site	Sp1	Sp2	Sp3	Sp4	Sp5	Sp6	Sp7	Sp8
A	0	5	1	0	13	11	1	1
B	1	7	1	0	6	31	0	6
C	2	21	2	0	24	32	0	2
D	0	3	1	3	19	27	3	1

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Figure 2. Workflow for Budgeting Using Climatic Debts and Credits. This example displays the general workflow for calculating climatic debt (left-hand side) and the credit that could be supplied by three possible scenarios (A–C) of pollutant reduction in a freshwater environment (right-hand side). The process starts with the temperature preferences of all species [species temperature indices (STIs)] calculated during a calibration period. The current community temperature index (CTI) is then calculated for each location by averaging the STIs of the species present; subtracting this value from the observed temperature quantifies the current debt (0.5°C). In this example, the potential effects of pollutant reduction (Δ*P*) are predicted using a process-based model of community structure developed during the calibration period, incorporating six forces shaping the community [33]. Predictions of community change for the three pollution reduction scenarios are made and converted into change in the CTI using the STIs. The difference between predicted CTIs and observed temperature quantifies the credits (equivalent to 0.1–0.6°C of cooling), completing the present-day climate budget. For a future budget, a process-based model is developed for the community response to warming and predictions made for a selected climate scenario, leading to estimates of increased debt (0.8°C). Updated predictions for the pollutant reductions, in light of warmer environmental temperatures, are then made (or for new interventions), leading to new credit estimates (0.1–0.5°C of cooling) and completing the future climate budget.

through analytical aspects such as combining data from different spatial scales and model selection, to the ways in which models are applied under novel environmental conditions [40,41]. In addition, factors such as habitat loss and invasive species may contribute to disequilibrium, and it could be challenging to distinguish climatic debt from these sources. Given the complexities of the different error sources and the potential for them to propagate, resampling methods are likely to be valuable for the quantification of uncertainty around debt and credit estimates [40,42]. For example, De Frenne *et al.* [4] modelled individual species' temperature response curves and then repeatedly sampled from these curves to estimate the CTI with confidence limits. Methods to estimate the overall disequilibrium, such as Markov chain and time series models [43,44], could also be valuable to place the climatic debt in a wider context (e.g., [8]).

Estimates of climatic credit run in parallel with debt (Figure 2). Credit is the difference between the inferred temperatures with and without management intervention (Figure 1). Typically, the aim is to estimate credits delivered by potential management interventions, but alternatively the consequences of past actions could be assessed. For example, a 0.9-mg l^{-1} reduction in the mean biochemical oxygen demand of English and Welsh rivers 1991–2011 is estimated to have contributed an environmental credit equivalent to 0.9°C of cooling [8]. Credit could be estimated by simple correlative methods that assume equilibrium between the community structure and the credit source (e.g., [8]), but process-based modelling would make more realistic predictions. For example, credit options that take time to be fully realised, such as restoration of tree cover for shading, will require models that capture transient dynamics and time lags.

Interventions such as increasing habitat connectivity or translocation of threatened populations [45] may alter the repayment rate. With process-based models, repayment rates are factored into the budget by making predictions of the change in debt by the assessment point (Figure 2), which may be before the **relaxation time** has elapsed. Repayment rates are predicted to vary along a continuum determined by the ecological traits of the species and the environmental conditions. Whereas some plant assemblages change very slowly and exhibit climatic debts as large as 10°C [23], freshwater invertebrate assemblages are highly responsive, and the species composition can change by 15–20% $year^{-1}$ in response to water temperature and quality [8].

Climate Accounting

The magnitude of ongoing climate change has precipitated a paradigm shift from trying to conserve current or historical conditions to managing ecosystem change [45,46] (Box 1). Climatic debts are likely to grow until a system converges to a new equilibrium state, perhaps involving catastrophic changes such as ecosystem collapse. Climatic credits could permanently offset portions of the debt by reducing the extent to which the equilibrium point moves, minimising biological change and risks of collapse (Figure 1). In such a dynamic system, budgets would be developed for explicit time points (e.g., 2050) forecasting the changes in both climate and biodiversity within the time window.

A basic climate budget could be assembled by assuming that sources of credit and debt are additive, allowing combinations of interventions to be appraised through simple summation (Figure 3). More refined versions employing process-based models could capture antagonistic or synergistic relationships among credit and debt sources. A budget could illustrate this by showing the net credit or debt resulting from management interventions applied separately and in combination. In addition to debt accrual from climate change, the budget could highlight other contributors, such as increased water extraction from river systems (Figure 3) or harvesting that could thin forest canopies, leading to higher maximum temperature [9]. In principle, budgets could be created across spatial scales ranging from local to national or international but will be most relevant where management interventions are feasible (primarily local or regional scales). Budgets could be averaged over a spatial extent (as in Figure 2) or calculated

Box 1. Conservation Strategies and Tackling the Climatic Debt

There is an emerging consensus that, given the magnitude of predicted climate change, ecosystems will change over the coming decades despite conservation efforts. In response, management can either accept the changes, with little or no intervention, or attempt to either steer the changes or slow them [54]. Management priorities may include increasing stability and adaptive capacity rather than trying to maintain the status quo from a previous climate [45,46].

In terms of the climatic budget, long-term biodiversity change is captured by ongoing drift of the equilibrium point towards higher temperatures (see Figure 1 in the main text). Climatic credits focus on limiting the shift in the equilibrium position, increasing community **resistance** to climate change. Altering the repayment rate changes the speed with which the observed community tracks the drifting equilibrium point, causing the debt to wax or wane (see Figure 1 in the main text).

Prober *et al.* [45] split climate change adaptations into four, reflecting quadrants based on two axes (Figure I): (i) interventions to ‘evade or ameliorate’ climate effects versus developing the adaptive capacity of ecosystems; and (ii) conservative, ‘low-regrets’ options versus more proactive and potentially risky ‘climate-targeted options’. Many credit options qualify as low regrets and aim to either ameliorate rising temperatures (e.g., restoring riparian tree cover for shading [55]) or increase adaptive capacity (e.g., by reducing co-occurring stressors [16]). Other credit options might involve compromises with ecosystem service provision, such as reducing the harvesting intensity in forests [56] or adopting smaller fishing quotas [57], or involve higher-risk interventions such as the active reshaping of local topography to alter microclimates and create refugia [15] or planting of non-native trees to cast deeper shade in forests [58].

Increasing repayment rates often involves higher-risk ‘climate-targeted’ actions, such as the translocation of warm-adapted species or genotypes (e.g., corals on the Great Barrier Reef [59]). The creation of habitat corridors [60] may span low- and high-risk categories, reflecting the potential for wider conservation benefits but also side effects (e.g., rapid convergence on an undesirable state). Options for reducing the repayment rate qualify as low regrets in the short term, acting to ameliorate rising temperatures, but failure to adapt may be higher risk in the long term. An example of this approach is augmenting existing populations of cooler-climate species to prevent local extinctions [45]. In practice, such repayment rate reductions might be combined with credit options (e.g., encouraging denser tree canopy cover [9]) to minimise change while the credit option is fully implemented.

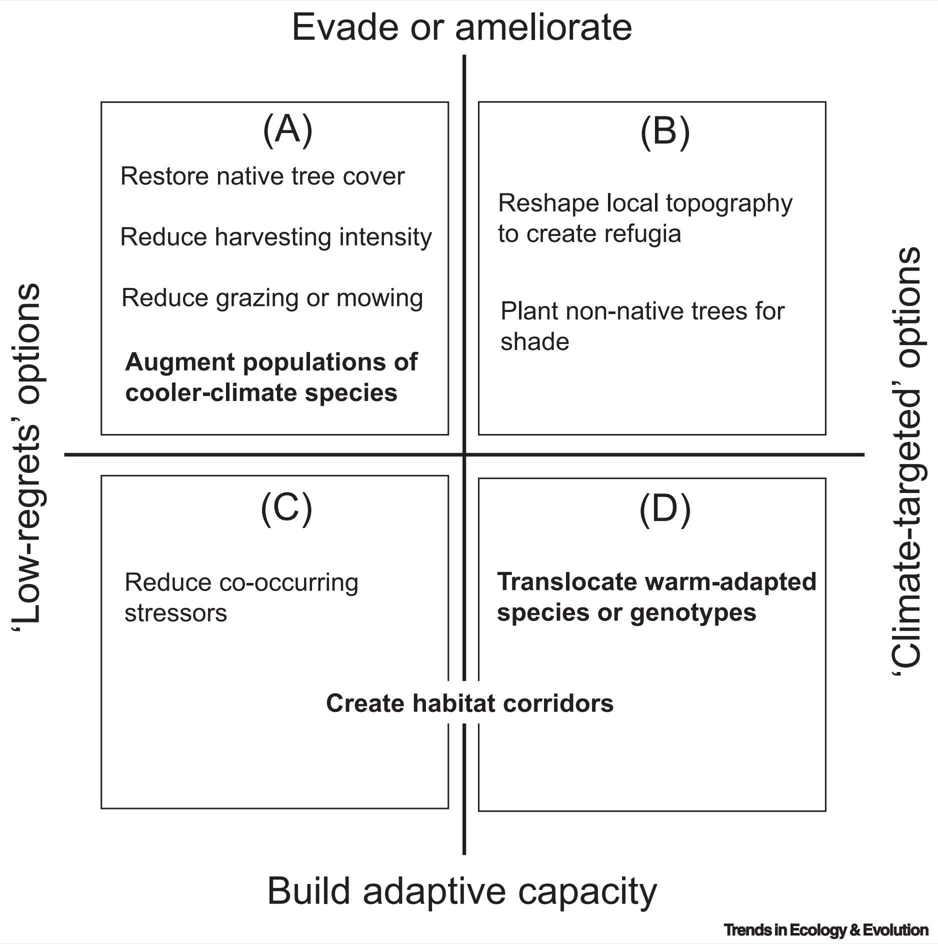

Figure I. Credit and Repayment Options Mentioned in the Text Classified into the Four Quadrants (A–D) on the Axes of Prober *et al.* [45]. Repayment options are distinguished by **italic** font.

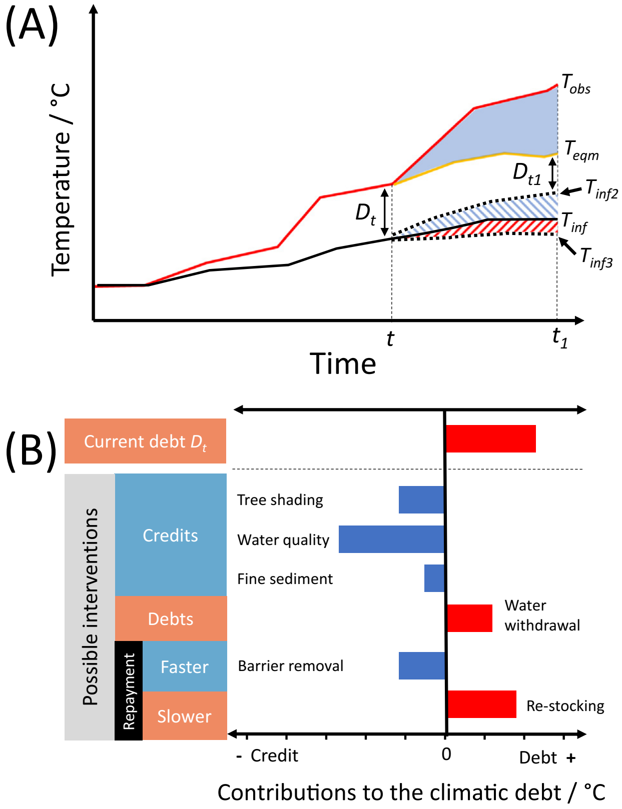

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Figure 3. Basic Accounting with Climatic Credits and Debts and Altered Repayment Rates. (A) Climatic debt (D) accumulates as the observed temperature (T_{obs}; unbroken red line) increases more rapidly than the inferred temperature (T_{inf}; unbroken black line). At the start of the period, the community is in equilibrium with the environment (overlapping lines). The debt is estimated at time t (D_t) after which measures are implemented to pay part of the debt with climatic credit (blue shading) and change the repayment rate (red and blue hatching). Climatic credit moves the equilibrium temperature (T_{eqm}; unbroken orange line) to a lower value than T_{obs}, while the repayment rate can be increased or decreased, leading to smaller (blue hatching; T_{inf2}) or larger (red hatching; T_{inf3}) debt by t_1 respectively (D_{t1}). T_{rec} is the endpoint at t_1 assuming a 'business-as-usual' scenario. (B) A hypothetical climate budget at t, comparing the estimated benefits of interventions for a river system. The expansion of riparian shading and the reduction of two stressors could accrue credit, while an increase in water withdrawal would add further debt. Interventions could either increase the repayment rate (e.g., removing barriers to increase connectivity) or decrease the rate (e.g., by maintaining cool-water salmonid populations via regular restocking), leading to smaller or larger debts, respectively. The effects of altered repayment rates are estimated for a fixed time period (e.g., 20 or 50 years), allowing rates to be converted to °C.

at the same resolution as the climate projections, producing maps for debt, different credit options, and the resultant net climatic debt.

Communities will have finite pools of climatic credit from the range of possible interventions. Pollutants could be eliminated or reduced to technological or financial limits; microclimates could be cooled by reduced grazing or mowing in grasslands or encouraging denser forest canopy, up until major changes in community structure are likely to occur [15]; and local refugia could be created within constraints such as space and cost, in addition to the physical limits on their cooling effect. In the short term, a budget may show net credit if the management intervention is sufficiently effective and the response rapid. For example, the 0.9°C of credit accrued by improving water quality in English and Welsh rivers (1991–2011) exceeded the 0.6°C of concomitant warming and was reflected by an increased prevalence of cooler-water taxa (e.g., Plecoptera [8]). However, any surplus will be temporary if climatic debt continues to mount and credit sources are exhausted, such that declines in cool-water species would be expected.

Many credit options qualify as **low-regrets interventions** [45], whereas others might involve compromises with ecosystem services or involve greater risks (Box 1). Altering the repayment rate could either minimise the debt and make a system more responsive to climate change or could temporarily slow the rate of change to allow more time for evolutionary adaptation [29] and the implementation of climatic credits (Box 1). In general, altering the repayment rate is likely to incur higher risks than supplying credit: increased repayment rates could encourage the system to move more rapidly to an undesirable state, while reduced rates would inflate the climatic debt, which could reduce ecosystem resilience [47] and incur greater risks of dramatic and unpredictable changes [28]. Consequently, the risk–reward trade-off of such approaches would need careful evaluation.

Concluding Remarks

Transient dynamics, such as climatic debt, are challenging to quantify and understand [21]. We propose a climatic credit–debt framework that builds on established concepts to assess impacts of warming and provide intuitive tools to evaluate adaptation options. Although this framework addresses the symptoms rather than the causes of climate warming, credits have the potential to reduce the magnitude of biodiversity changes at local or regional scales and increase the scope for adaptation. Minimising climatic debts may also increase the resilience of the system to pulse disturbances (e.g., climate variability). The climatic debt concept is being used increasingly in ecology and the climatic credit idea has recently been demonstrated empirically [8]. The next step is to bring these together into a climatic budget for a model system to assess the full value of the approach.

Research priorities encompass both conceptual and applied issues (see Outstanding Questions). Many centre on improving debt and credit forecasting and on ways to limit model complexity. Most climatic debt studies have addressed community-level responses but could generalise from species to ecosystems and biomes (including ecosystem services [48]) and into a broader context alongside other drivers of environmental change, including land-use change and nutrient enrichment. A few recent studies (e.g., [5,23,49–51]) have started to look at factors mitigating or amplifying the debt, and this is an area that will benefit from more work. Debts and credits can also be quantified on multivariate axes (e.g., temperature and precipitation [52]), which could be valuable for some systems, albeit at the expense of a simple currency (e.g., °C or mm year^{-1}). Going further, budgets could be built for other stressors, such as nutrient concentrations (e.g., creating a budget with units of mg l^{-1} in aquatic environments).

From a management perspective, the efficacy of climatic credits is likely to vary among ecosystems and locations. Different interventions will be possible in different systems, based on both the nature of the system and wider landscape and the technical and financial feasibility. The validity of credits depends on how closely they replicate community responses to declining temperatures. It is expected that the best results will be achieved when temperature itself is modified (e.g., by shading) or where there is a mechanistic relationship between the biotic variables, temperature, and the potential source of climatic credit. For example, Vaughan and Gotelli [8] related aquatic invertebrate community structure to temperature and water quality improvement, both of which affect oxygen stress [53]. Ultimately, credit sources are finite: once a stressor is eliminated or reduced to a feasible minimum, the credit source will be exhausted. In many ecosystems, climate warming will eventually exceed the available credit, so the aim is to minimise the overall magnitude of change. Our hope is that this general framework of climatic debt and credits will contribute to the understanding and forecasting of the potential value of local interventions to reduce climate change impacts [17].

Outstanding Questions

Where are climatic debts likely to be greatest? The answer will depend on both ecological traits (e.g., body size, plasticity) and environmental characteristics (e.g., topography, habitat area).

To what extent do ecological and evolutionary processes act to write off climatic debts?

How do different biological processes and environmental conditions on the leading and trailing edges of species' geographic ranges interact to determine transient dynamics and relaxation times?

Can the same model structure be used across communities and ecosystems or are bespoke models required?

To what extent can demographic responses to changing climate be generalised across taxa (e.g., using trait or phylogenetic data) to minimise data requirements for process-based climatic debt modelling?

What are the most effective approaches for partitioning the total disequilibrium (environmental lag) between climatic debt and other sources (e.g., habitat loss)?

How can other facets of climate change (e.g., extreme events, multiple climate variables) be incorporated into a climatic debt framework?

How much climatic credit could be supplied to different ecosystems and at what point will climatic credit be exhausted?

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