Citation for final published version:

Vaughan, Ian P. and Gotelli, Nicholas J. 2021. Using climatic credits to pay the climatic debt. Trends in Ecology and Evolution 36 (2) , pp. 104-112. 10.1016/j.tree.2020.10.002 file

Publishers page: http://dx.doi.org/10.1016/j.tree.2020.10.002 <http://dx.doi.org/10.1016/j.tree.2020.10.002>

Using climatic credits to pay the climatic debt

Ian P. Vaughan[1*] & Nicholas J. Gotelli[2]

[1]School of Biosciences, Cardiff University, Cardiff, CF10 3AX, UK.
[2]Department of Biology, University of Vermont, Burlington, VT 05405, USA.

*Correspondence: I.P. Vaughan (vaughanip@cardiff.ac.uk)
Twitter: @IanVaughan21

Keywords: climate change; adaptation; extinction debt; transient dynamics

Abstract

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 over-optimistic 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.

Climatic debt, 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; Fig 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 could be more important than temperature, such as precipitation [11] or seasonal maxima [9]. For simplicity, we focus on average temperatures, but climatic debt could equally be quantified in other units (e.g. mm precipitation yr^{-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], and by relatively slow changes in abundance amongst 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 under-estimates 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 down, such as reducing 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] (Fig 1). In the long-term, rising temperatures are likely to exceed the credits, but they should still reduce the overall magnitude 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** (Fig 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 for understanding 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

Estimating climatic debt begins with quantifying the relationship between community structure and temperature, so that temperature can be inferred from the observed species composition (Figs 1 & 2). The most common approach is to calculate the **community temperature index** (CTI) from the **species temperature indices** 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] (Figs 1 & 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 (Fig 1). Calculating a future climatic debt follows the same process, using predicted climate and community structure (Fig 2).

Estimating climatic debt is simple in principle, but it involves at least three important methodological challenges. The first is obtaining 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 augmenting or corroborating distribution data with experimental data [26,27] and modelling 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, 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 developing realistic non-equilibrium 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 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]). Developing 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 implementing these models is controlling model complexity and obtaining data to estimate process-based parameters [33]: expanding species-level phylogenies and databases of ecological traits may help to interpolate missing demographic data [38].

The third challenge is quantifying and reducing 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, 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 different error sources and the potential for them to propagate up, resampling methods are likely to be valuable for quantifying 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 to debt (Fig 2). Credit is the difference between the inferred temperatures with and without management intervention (Fig 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 which assume equilibrium between 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 restoring tree cover for shading, will require models that capture transient dynamics and time lags.

Interventions such as increasing habitat connectivity or translocating 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 (Fig 2), which may be before the **relaxation time** has elapsed. Repayment rates are predicted to vary along a continuum determined by 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 species composition can change 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 (Fig 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 (Fig 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 increasing water extraction from river systems (Fig 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 Fig 2) or calculated 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, before 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. Plectoptera [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 implementation of climate 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, whilst reduced rates would inflate the climatic debt which could reduce ecosystem resilience [47] and incur greater risks of dramatic and unpredictable changes [28]. As a consequence, 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 for evaluating 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 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 yr^{-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 both upon the nature of the system and wider landscape, and technical and financial feasibility. The validity of credits depends upon 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 climate 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 understanding and forecasting the potential value of local interventions to reduce climate change impacts [17].

Acknowledgements

Our thanks to Pieter De Frenne, two anonymous referees and the editor for helpful comments on a previous version.

References

1. Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst*. 37, 637–669
2. Bertrand, R. *et al*. (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479, 517–520.
3. Devictor, V. *et al*. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* 2, 121–124.
4. De Frenne, P. et al. (2013) Microclimate moderates plant responses to macroclimate warming. *P. Natl. Acad. Sci. USA* 110, 18561–18565.
5. Bertrand, T. *et al*. (2016) Ecological constraints increase the climatic debt in forests. *Nat. Commun.* 7, 12643.
6. Fadrique, B. *et al*. (2018) Widespread but heterogeneous responses of Andean forests to climate change. *Nature* 564, 207–212.
7. Auffret, A.G. and Thomas, C.D. (2019) Synergistic and antagonistic effects of land use and non-native species on community responses to climate change. *Global Change Biol.* 25, 4303–4314.
8. Vaughan, I.P. and Gotelli, N.J. (2019) Water quality improvements offset the climatic debt for stream macroinvertebrates over twenty years. *Nat. Commun.* 10, 1956.
9. Zellweger, F. *et al*. (2020) Forest microclimate dynamics drive plant responses to warming. *Science* 368, 772–775.
10. Svenning, J.-C. and Sandel, B. (2013) Disequilibrium vegetation dynamics under future climate change. *Am. J. Bot.* 100, 1266–1286.

11. Boyle, W.A. *et al.* (2020) Hygric niches for tropical endotherms. *TREE*, in press.

12. Alexander, J.M. *et al.* (2017) Lags in the response of mountain plant communities to climate change. *Global Change Biol.* 24, 563–579.

13. Hylander, K. & Ehrlén, J. (2013) The mechanisms causing extinction debts. *TREE*, **28**, 341-346.

14. Haase, P. *et al.* (2019) Moderate warming over the past 25 years has already reorganized stream invertebrate communities. *Sci. Total Environ.* 658, 1531–1538.

15. Greenwood, O. *et al.* (2018) Reviewing *in situ* management to conserve biodiversity under climate change. *J. Appl. Ecol*. 53, 885–894.

16. Kosten, S. *et al.* (2012) Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biol.* 18, 118–126.

17. Scheffer, M. *et al.* (2015) Creating a safe operating space for iconic ecosystems. *Science* 347, 1317–1319.

18. Bland, L.M. *et al*. (2018) Developing a standardized definition of ecosystem collapse for risk assessment. *Front. Ecol. Environ*. 16, 29–36.

19. Jackson, S.T. and Sax, D.F. (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *TREE* 25, 153-160.

20. Essl, F. *et al*. (2015) Delayed biodiversity change: no time to waste. *TREE* 30, 375–378.

21. Hastings, A. *et al.* (2018) Transient phenomena in ecology. *Science* 361, eaat6412.

22. Watts, K. *et al* (2020) Ecological time lags and the journey towards conservation success. *Nat. Ecol. Evol.* 4, 304–311.

23. Gaüzère, P. *et al.* (2018) Empirical predictability of community responses to climate change. *Front. Ecol. Evol.* 6, 186.

24. Devictor. V. *et al.* (2008) Birds are tracking climate warming, but not fast enough. *Proc. R. Soc. B* 275, 2743–2748.

25. Tilman, D. *et al.* (1994) Habitat destruction and the extinction debt. *Nature* 371, 65–66.

26. Alexander, J.M. *et al.* (2016) When climate reshuffles competitors: a call for experimental macroecology. *TREE* 31, 831–841.

27. Kotta, J. *et al*. (2019) Integrating experimental and distribution data to predict future species patterns. *Sci. Rep*. 9, 1821.

28. Blonder, B. *et al*. (2017) Predictability in community dynamics. *Ecol. Lett.* 20, 293–306.

29. Radchuk, V. *et al*. (2019) Adaptive responses of animals to climate change are most likely insufficient. *Nat. Commun.* 10, 3109.

30. Peterson, M.L. *et al*. (2019) Incorporating local adaptation into forecasts of species' distribution and abundance under climate change. *Global Change Biol.* 25, 775–793.

31. Liu, H. *et al*. (2020) Climatic-niche evolution follows similar rules in plants and animals. *Nat. Ecol. Evoln*. 4, 753–763.

32. Román-Palacios, C. and Wiens, J.J. (2020) Recent responses to climate change reveal the drivers of species extinction and survival. *Proc. Natl. Acad. Sci. U.S.A.* 117, 4211–4217.

33. Urban, M.C. *et al*. (2016) Improving the forecast for biodiversity under climate change. *Science* 353, aad8466.

34. Dullinger, S. *et al*. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. *Nat. Clim. Change* 2, 619–622.

35. Cotto, O. *et al*. (2017) A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. *Nat. Commun.* 8, 15399.

36. Talluto, M.V. *et al*. (2017) Extinction debt and colonization credit delay range shifts of eastern North American trees. *Nat. Ecol. Evol.* 1, 0182.

37. D'Amen, M. *et al*. (2017) Spatial predictions at the community level: from current approaches to future frameworks. *Biol. Rev*. 92, 169–187.

38. Evans, M.E.K. *et al*. (2016) Towards process-based range modeling of many species. *TREE* 31, 860–871.

39. Briscoe, N.J. *et al*. (2019) Forecasting species range dynamics with process-explicit models: matching methods to applications. *Ecol. Lett.* 22, 1940–1956.

40. Beale, C.M. and Lennon, J.J. (2012) Incorporating uncertainty in predictive species distribution modelling. *Philos. Trans. R. Soc. London, Ser. B* 367, 247–258.

41. Araújo, M.B. *et al*. (2019) Standards for distribution models in biodiversity assessments. *Sci. Adv*. 5, eaat4858.

42. Rodríguez-Sánchez, F. *et al*. (2012). Uncertainty in thermal tolerances and climatic debt. *Nat. Clim. Change* 2, 638–639.

43. Hill, M.F. *et al*. (2002) Spatio-temporal variation in Markov chain models of subtidal community succession. *Ecol. Lett*. 5, 665–675.

44. Ives, A.R. *et al*. (2003) Estimating community stability and ecological interactions from time-series data. *Ecol. Monogr.* 73, 301–330.

45. Prober, S.M. *et al*. (2019) Shifting the conservation paradigm: a synthesis of options for renovating nature under climate change. *Ecol. Monogr.* 89, e01333.

46. Dudney, J. *et al*. (2018) Navigating novelty and risk in resilience management. *TREE*, 33, 863–873.

47. Mariani, M. *et al*. (2019) Climate change reduces resilience to fire in subalpine rainforests. *Global Change Biol.* 25, 2030–2042.

48. Isbell, F. *et al*. (2015) The biodiversity-dependent ecosystem service debt. *Ecol. Lett.* 18, 119–134.

49. Gaüzère, P. *et al.* (2017) Where do they go? The effects of topography and habitat diversity on reducing climatic debt in birds. *Global Change Biol.* 23, 2218–2229.

50. Lewthwaite, J.M.M. *et al*. (2018) Canadian butterfly climate debt is significant and correlated with range size. *Ecography* 41, 2005–2015.

51. Bertrand, T. (2019) Unequal contributions of species' persistence and migration on plant communities' response to climate warming throughout forests. *Ecography* 42, 211–213.

52. Blonder, B.*et al*. (2015) Linking environmental filtering and disequilibrium to biogeography with a community climate framework. *Ecology* 96, 972–985.

53. Verberk, W.C.E.P. *et al*. (2016) Field and laboratory studies reveal interacting effects of stream oxygenation and warming on aquatic ectotherms. *Global Change Biol.* 22, 1769–1778.

54. Aplet, G.H. and McKinley, P.S. (2017) A portfolio approach to managing ecological risks of global change. *Ecosyst. Health Sustainability*, 3, e01261.
55. Wondzell, S.M. *et al*. (2019) What matters most: are future stream temperatures more sensitive to changing air temperatures, discharge, or riparian vegetation? *J. Am. Water Resour. Assoc*. 55, 116–132.
56. Scheffer, M. *et al*. (2018) A global climate niche for giant trees. *Global Change Biol.* 24, 2875–2883.
57. Voss, R. *et al*. (2019) Ecological-economic sustainability of the Baltic cod fisheries under ocean warming and acidification. *J. Environ. Manage*. 238, 110–118.
58. Zellweger, F. *et al*. (2019) Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe.
59. Quigley, K.M. *et al*. (2019) The active spread of adaptive variation for reef resilience. *Ecol. Evol*. 9, 11122–11135.
60. McGuire, J.L. *et al*. (2016) Achieving climate connectivity in a fragmented landscape. *PNAS* 113, 7195–7200.

Figure legends

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): ΔE 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 only moved part 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 ΔE and *D* to 1.0 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 (dashed white line = original basin shape), reducing relaxation times: although ΔE is 1.5°C as in panel B, *D* is only 0.5°C.

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 (ΔP) 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 by 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.

Figure 3. Basic accounting with climatic credits, debts and altered repayment rates. (**A**) Climatic debt, *D*, accumulates as the observed temperature (T_{obs}; solid red line) increases more rapidly than the reconstructed temperature (T_{rec}; solid 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 (solid blue shading) and change the repayment rate (red and blue hatching). Climatic credit moves the equilibrium temperature (T_{eqm}; solid orange line) to a lower value than T_{obs}, whilst the repayment rate can be increased or decreased, leading to smaller (blue hatching; T_{r2}) or larger (red hatching; T_{r3}) 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 reduction of two stressors could accrue credit, whilst 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 re-stocking), 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 a rate to be converted to °C.

Figure legend for Box 1

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.

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 coming decades in spite of 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 (Fig 1). 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 (Fig 1).

Prober *et al*. [45] split climate change adaptations into four, reflecting quadrants based on two axes (Fig 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 either to 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 actively reshaping local topography to alter microclimates and create refugia [15], or planting non-native trees to cast deeper shade in forests [58].

Increasing repayment rates often involves higher risk ‘climate-targeted’ actions, such as translocating warm-adapted species or genotypes (e.g. corals on the Great Barrier Reef [59]). Creating 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 whilst the credit option is fully implemented.

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 species temperature index 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 to biodiversity or ecosystem service provision.
- **Process-based models** – mechanistic models of community structure that incorporate aspects of colonization, population growth, species interactions and extinction. Such models can make predictions under both equilibrium and non-equilibrium 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 yr^{-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.

Fig 1.

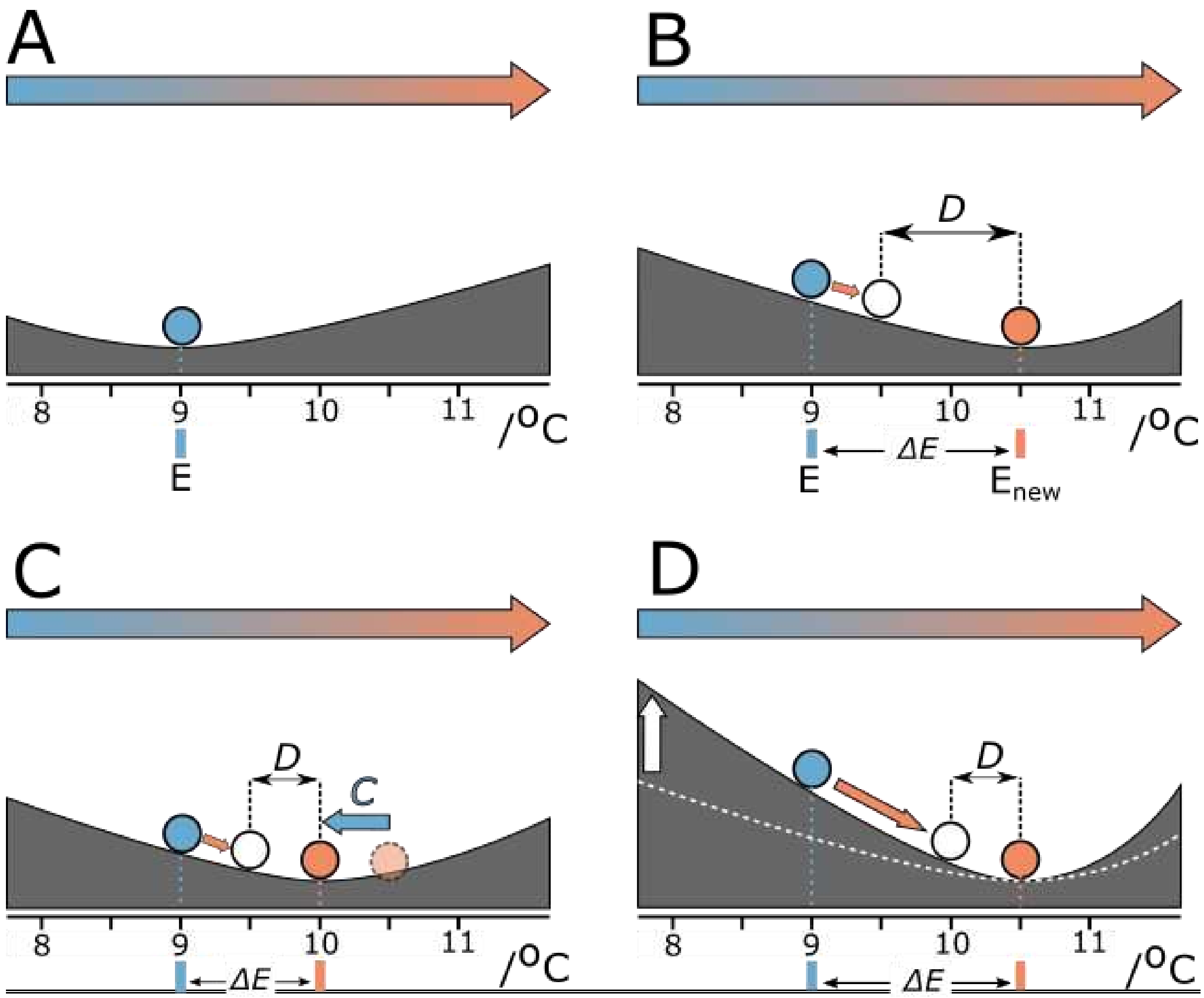


Fig 2.

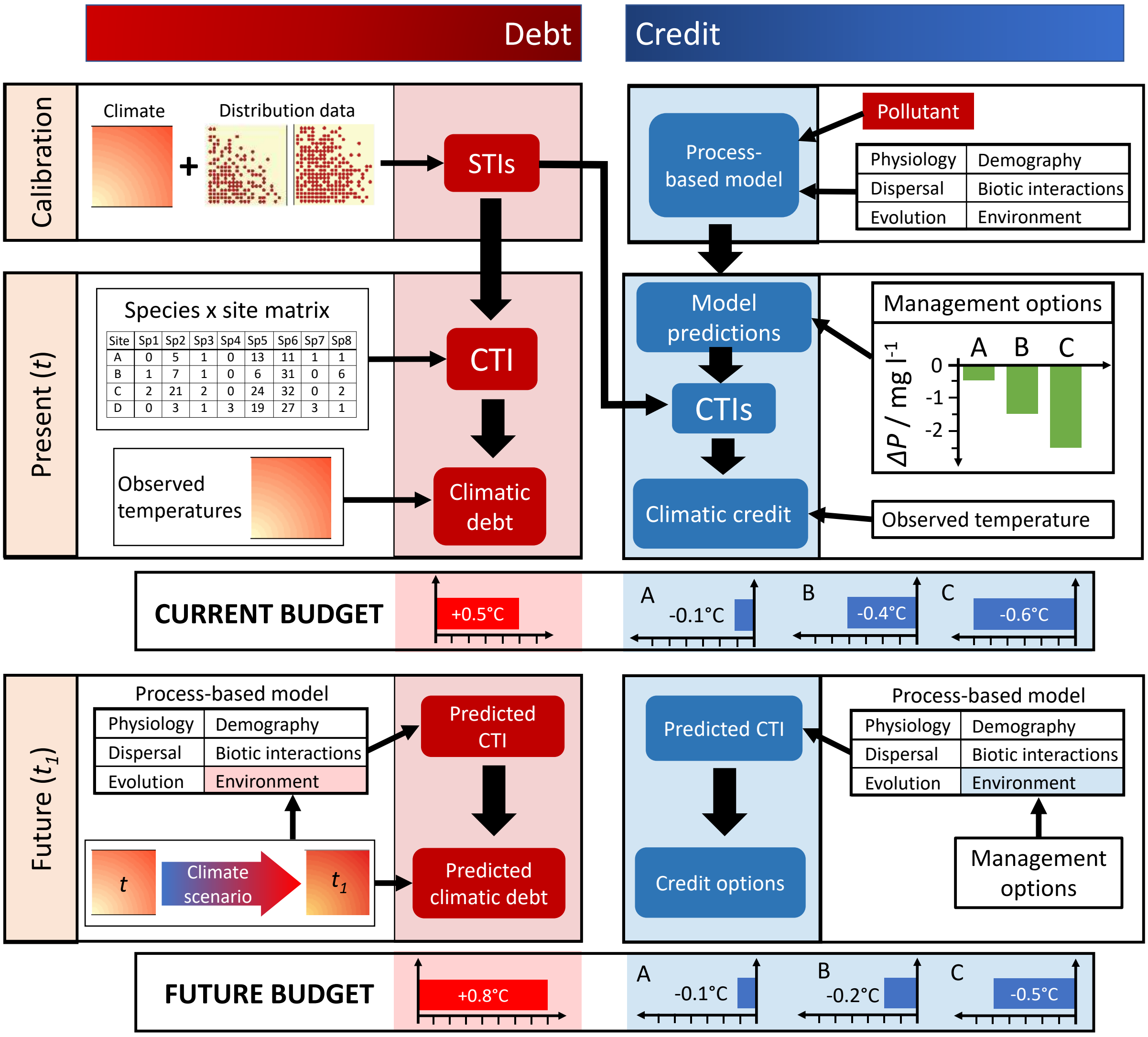

Debt
Credit
Calibration
Climate
Distribution data
+
STIs
Pollutant
Process-based model
Physiology
Demography
Dispersal
Biotic interactions
Evolution
Environment
Present (t)
Species x site matrix
Site Sp1 Sp2 Sp3 Sp4 Sp5 Sp6 Sp7 Sp8
A 0 5 1 0 13 11 1 1
B 1 7 1 0 6 31 0 6
C 2 21 2 0 24 32 0 2
D 0 3 1 3 19 27 3 1
CTI
Observed temperatures
Climatic debt
Model predictions
CTIs
Climatic credit
Management options
ΔP / mg l-1
A B C
0
-1
-2
Observed temperature
CURRENT BUDGET
+0.5°C
A -0.1°C
B -0.4°C
C -0.6°C
Future (t1)
Process-based model
Physiology
Demography
Dispersal
Biotic interactions
Evolution
Environment
t
Climate scenario
t1
Predicted CTI
Predicted climatic debt
Predicted CTI
Credit options
Process-based model
Physiology
Demography
Dispersal
Biotic interactions
Evolution
Environment
Management options
FUTURE BUDGET
+0.8°C
A -0.1°C
B -0.2°C
C -0.5°C

Fig 3

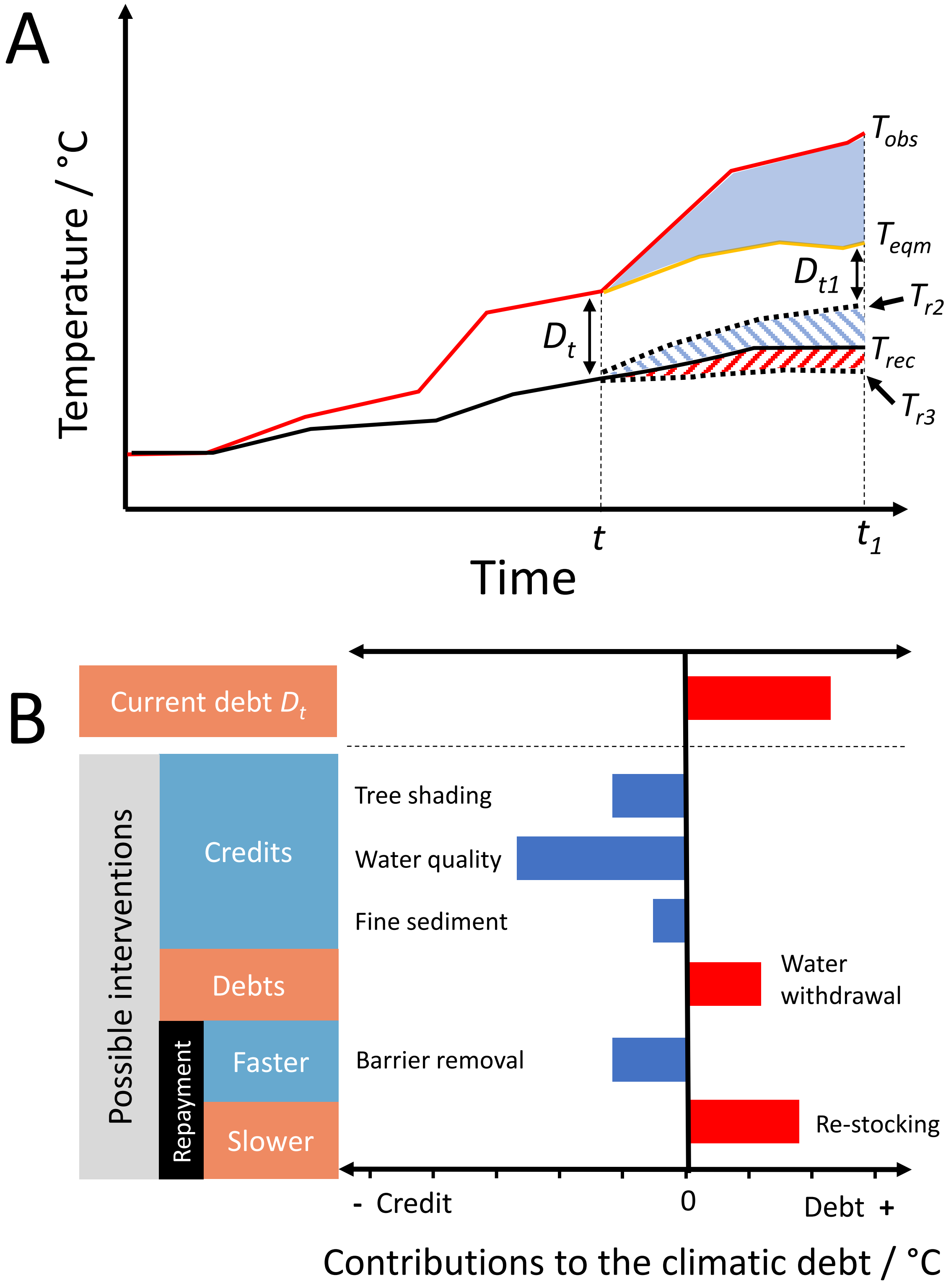
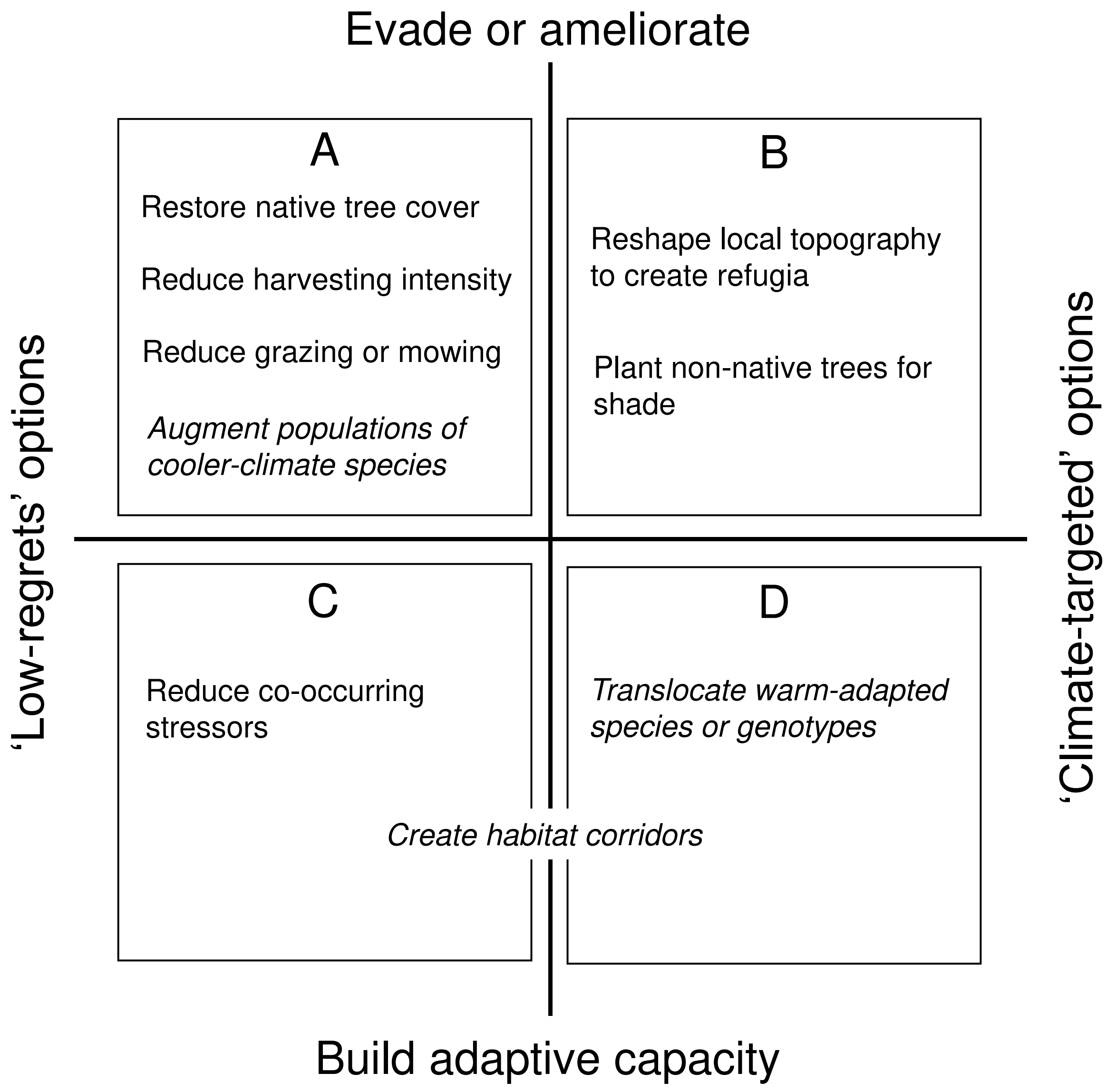

A
Temperature / °C
T_{obs}
T_{eqm}
D_{t1}
T_{r2}
D_t
T_{rec}
T_{r3}
t
t_1
Time
B
Current debt D_t
Possible interventions
Credits
Debts
Repayment
Faster
Slower
Tree shading
Water quality
Fine sediment
Water withdrawal
Barrier removal
Re-stocking
- Credit
0
Debt +
Contributions to the climatic debt / °C

Fig I.


Evade or ameliorate
A
Restore native tree cover
Reduce harvesting intensity
Reduce grazing or mowing
Augment populations of cooler-climate species
B
Reshape local topography to create refugia
Plant non-native trees for shade
'Low-regrets' options
'Climate-targeted' options
C
Reduce co-occurring stressors
D
Translocate warm-adapted species or genotypes
Create habitat corridors
Build adaptive capacity