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2 3	Using climatic credits to pay the climatic debt
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10 11 12 13	*Correspondence: I.P. Vaughan (vaughanip@cardiff.ac.uk) Twitter: @IanVaughan21
14 15 16 17	Keywords: climate change; adaptation; extinction debt; transient dynamics
18 19	Abstract
20	Many organisms are accumulating climatic debt as they respond more slowly than expected
21	to rising global temperatures, leading to disequilibrium of species diversity with
22	contemporary climate. The resulting transient dynamics are complex and may cause over-
23	optimistic biodiversity assessments. We propose a simple budget framework to integrate
24	climatic debt with two classes of intervention: i) climatic credits that pay some of the debt,
25	reducing the overall biological change required to reach a new equilibrium, and ii) options to
26	adjust the debt repayment rate, either making a system more responsive by increasing the
27	rate or temporarily reducing the rate to buy more time for local adaptation and credit
28	implementation. We illustrate how this budget can be created and highlight limitations and
29	challenges.
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#### 35 Climatic debt, credit and the value of budgeting

36 In response to climate change, organisms must migrate, adapt via phenotypic or 37 evolutionary mechanisms, or face extinction [1]. Across many parts of the world and a range 38 of taxa, changes in species' distributions following recent decades of climate change have 39 been smaller than expected. The difference between observed and expected changes is 40 described as **climatic debt** (see Glossary; Fig 1), which is "repaid" when biodiversity 41 reaches equilibrium with the new climate. The prime focus of such analyses has been rising 42 temperatures. Recent studies suggest that climatic debt in contemporary plant and animal 43 assemblages could be equivalent to  $\sim 0.4-1.3^{\circ}$ C of warming or more (e.g. [2–9]), and there is 44 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 45 precipitation [11] or seasonal maxima [9]. For simplicity, we focus on average temperatures, 46 47 but climatic debt could equally be quantified in other units (e.g. mm precipitation  $yr^{-1}$  [7]). 48

Climatic debts can be generated by limits to the rates of dispersal and establishment of more 49 50 thermophilic species, by the slow loss of cooler-climate species [12], and by relatively slow 51 changes in abundance amongst species that persist with increasing temperatures. The total debt may be influenced by numerous factors, including species' traits and landscape 52 properties [5], which vary across spatial and temporal scales, and levels of biological 53 organisation [13]. Although some taxa appear able to keep pace with temperature changes 54 55 (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. 56

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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].

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Inspired by Jackson and Sax's [19] 'biodiversity budget', in which extinction debt is 69 70 balanced against immigration credit, we outline a framework uniting climatic debts, credits, 71 and factors that could affect the **repayment rate** (Fig 1). Although a climatic budget is a 72 greatly simplified view of the manifold influences on species distributions, it would be valuable for communicating with practitioners, conservation organisations, policy makers, 73 74 and other stakeholders including the general public [19]. The forecasts from climate models 75 are familiar to these groups, with time series of predicted temperature increases and maps 76 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 77 environmental change, biodiversity responses, and the extent to which management 78 79 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 80 81 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 82 83 ecological responses [20-22]. However, these lags are challenging to quantify and 84 communicate in simple terms, and are frequently overlooked, leading to biased assessments 85 of biodiversity.

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#### 88 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

91 composition (Figs 1 & 2). The most common approach is to calculate the **community** 92 temperature index (CTI) from the species temperature indices of the species present e.g. 93 [3,6,7,23,24]. To calculate the current climatic debt, the inferred temperature (e.g. CTI) is 94 subtracted from the observed environmental temperature [2] (Figs 1 & 2): this is analogous 95 to the difference between the observed and expected species richness for extinction debt 96 [25]. Indebted communities have a greater frequency or abundance of cooler-climate 97 species than expected, leading to an inferred temperature that is below the observed 98 temperature (Fig 1). Calculating a future climatic debt follows the same process, using 99 predicted climate and community structure (Fig 2).

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Estimating climatic debt is simple in principle, but it involves at least three important 101 102 methodological challenges. The first is obtaining reliable estimates of temperature 103 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 104 generate novel communities and novel species interactions, leading to changes in the 105 apparent relationships between temperature and species occurrence [26]. Possible solutions 106 107 here include augmenting or corroborating distribution data with experimental data [26,27] and modelling climate preferences without assuming equilibrium (see below). An added 108 109 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 110 111 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 112 assessment and forecasting. 113

114

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. 119 The solution is to adopt more mechanistic models that incorporate the biological processes 120 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 121 122 made. Some researchers have extended conventional species distribution models to 123 incorporate mechanisms such as dispersal and then 'stacked' individual species' predictions 124 to estimate community structure. More recently, full process-based models have been 125 used to generate forecasts [37–39]. The challenge for implementing these models is 126 controlling model complexity and obtaining data to estimate process-based parameters [33]: 127 expanding species-level phylogenies and databases of ecological traits may help to interpolate missing demographic data [38]. 128

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The third challenge is quantifying and reducing uncertainty in estimates of temperature 130 131 preferences and community responses to climate change. Uncertainty may be introduced at numerous points, from limitations in species distribution data and uncertainty around climate 132 forecasts, through analytical aspects such as combining data from different spatial scales 133 and model selection, to the ways in which models are applied under novel environmental 134 135 conditions [40,41]. In addition, factors such as habitat loss and invasive species may 136 contribute to disequilibrium, and it could be challenging to distinguish climatic debt from 137 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 138 139 around debt and credit estimates [40,42]. For example, De Frenne et al. [4] modelled 140 individual species' temperature response curves, and then repeatedly sampled from these curves to estimate the CTI with confidence limits. Methods to estimate the overall 141 142 disequilibrium, such as Markov chain and time series models [43,44], could also be valuable 143 to place the climatic debt in a wider context (e.g. [8]).

144

Estimates of climatic credit run in parallel to debt (Fig 2). Credit is the difference between theinferred temperatures with and without management intervention (Fig 1). Typically, the aim is

147 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<sup>-1</sup> reduction in the 148 149 mean biochemical oxygen demand of English and Welsh rivers 1991-2011 is estimated to 150 have contributed an environmental credit equivalent to 0.9°C of cooling [8]. Credit could be 151 estimated by simple correlative methods which assume equilibrium between community 152 structure and the credit source e.g. [8], but process-based modelling would make more 153 realistic predictions. For example, credit options that take time to be fully realised, such as 154 restoring tree cover for shading, will require models that capture transient dynamics and time 155 lags.

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Interventions such as increasing habitat connectivity or translocating threatened populations 157 [45] may alter the repayment rate. With process-based models, repayment rates are factored 158 159 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 160 vary along a continuum determined by ecological traits of the species and the environmental 161 conditions. Whereas some plant assemblages change very slowly and exhibit climatic debts 162 163 as large as 10°C [23], freshwater invertebrate assemblages are highly responsive, and species composition can change 15–20% year<sup>-1</sup> in response to water temperature and 164 165 quality [8].

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#### 168 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 thechanges in both climate and biodiversity within the time window.

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178 A basic climate budget could be assembled by assuming that sources of credit and debt are 179 additive, allowing combinations of interventions to be appraised through simple summation 180 (Fig 3). More refined versions employing process-based models could capture antagonistic 181 or synergistic relationships among credit and debt sources. A budget could illustrate this by 182 showing the net credit or debt resulting from management interventions applied separately 183 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 184 harvesting that could thin forest canopies, leading to higher maximum temperature [9]. In 185 principle, budgets could be created across spatial scales ranging from local to national or 186 187 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 188 Fig 2) or calculated at the same resolution as the climate projections, producing maps for 189 debt, different credit options and the resultant net climatic debt. 190

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Communities will have finite pools of climatic credit from the range of possible interventions. 192 193 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 194 canopy, before major changes in community structure are likely to occur [15]; and local 195 196 refugia could be created within constraints such as space and cost, in addition to the 197 physical limits on their cooling effect. In the short term, a budget may show net credit if the 198 management intervention is sufficiently effective and the response rapid. For example, the 199 0.9°C of credit accrued by improving water quality in English and Welsh rivers (1991-2011) 200 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 201

202 debt continues to mount and credit sources are exhausted, such that declines in cool-water203 species would be expected.

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205 Many credit options qualify as **low-regrets interventions** [45], whereas others might involve 206 compromises with ecosystem services or involve greater risks (Box 1). Altering the 207 repayment rate could either minimise the debt and make a system more responsive to 208 climate change or could temporarily slow the rate of change to allow more time for 209 evolutionary adaptation [29] and implementation of climate credits (Box 1). In general, 210 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, 211 whilst reduced rates would inflate the climatic debt which could reduce ecosystem resilience 212 [47] and incur greater risks of dramatic and unpredictable changes [28]. As a consequence, 213 214 the risk-reward trade-off of such approaches would need careful evaluation.

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## 217 Concluding remarks

218 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 219 220 impacts of warming and provide intuitive tools for evaluating adaptation options. Although 221 this framework addresses the symptoms rather than the causes of climate warming, credits 222 have the potential to reduce the magnitude of biodiversity changes at local or regional 223 scales, and increase the scope for adaptation. Minimising climatic debts may also increase 224 the resilience of the system to pulse disturbances (e.g. climate variability). The climatic debt 225 concept is being used increasingly in ecology and the climatic credit idea has recently been 226 demonstrated empirically [8]. The next step is to bring these together into a climatic budget 227 for a model system to assess the full value of the approach.

229 Research priorities encompass both conceptual and applied issues (see Outstanding 230 Questions). Many centre on improving debt and credit forecasting, and ways to limit model 231 complexity. Most climatic debt studies have addressed community-level responses, but 232 could generalise from species to ecosystems and biomes (including ecosystem services 233 [48]) and into a broader context alongside other drivers of environmental change, including 234 land use change and nutrient enrichment. A few recent studies (e.g. [5,23,49-51]) have 235 started to look at factors mitigating or amplifying the debt, and this is an area that will benefit 236 from more work. Debts and credits can also be quantified on multivariate axes (e.g. 237 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<sup>-1</sup>). Going further, budgets could be built for 238 other stressors, such as nutrient concentrations (e.g. creating a budget with units of mg l<sup>-1</sup> in 239 aquatic environments). 240

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From a management perspective, the efficacy of climatic credits is likely to vary among 242 ecosystems and locations. Different interventions will be possible in different systems, based 243 both upon the nature of the system and wider landscape, and technical and financial 244 245 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 246 247 when temperature itself is modified (e.g. by shading) or where there is a mechanistic 248 relationship between the biotic variables, temperature, and the potential source of climate 249 credit. For example, Vaughan and Gotelli [8] related aquatic invertebrate community 250 structure to temperature and water quality improvement, both of which affect oxygen stress 251 [53]. Ultimately, credit sources are finite: once a stressor is eliminated or reduced to a 252 feasible minimum, the credit source will be exhausted. In many ecosystems, climate 253 warming will eventually exceed the available credit, so the aim is to minimise the overall 254 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 255 reduce climate change impacts [17]. 256

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- 385

#### 387 Figure legends

388

389 Figure 1: Basic principles of climatic debt and credit, and repayment rate, using the familiar 390 ball-in-landscape analogy. Equilibrium community composition changes across the x-axis, with the 391 relative abundance of species favouring warm temperatures increasing from left to right. (A) The 392 system is at equilibrium (E) prior to climate warming, with the blue ball sitting at the bottom of the 393 valley. (B) 1.5°C of warming changes the landscape, shifting the equilibrium point to the right ( $E_{new}$ ) 394 red ball):  $\Delta E$  represents the biological change between E and  $E_{new}$ . The community (white ball) 395 responds to the change, moving to the right, but at the time of observation has only moved part way 396 towards  $E_{new}$ : the distance by which it falls short is the climatic debt (*D*), which is equal to 1°C here. 397 (C) Climatic credit (C) offsets 0.5°C of the warming (e.g. via improved water quality), reducing  $\Delta E$  and 398 D to 1.0 and 0.5°C respectively, and increasing the community's resistance. (D) Measures to alter the 399 repayment rate change the steepness of the valley sides. In this example, increased habitat 400 connectivity creates a steeper-sided basin (dashed white line = original basin shape), reducing 401 relaxation times: although  $\Delta E$  is 1.5°C as in panel B, D is only 0.5°C.

402

403 Figure 2: Workflow for budgeting using climatic debts and credits. This example displays the 404 general workflow for calculating climatic debt (left-hand side) and the credit that could be supplied by 405 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; 406 407 STIs) calculated during a calibration period. The current community temperature index (CTI) is then 408 calculated for each location by averaging the STIs of the species present: subtracting this value from 409 the observed temperature quantifies the current debt  $(0.5^{\circ}C)$ . In this example, the potential effects of 410 pollutant reduction ( $\Delta P$ ) are predicted using a process-based model of community structure, developed during the calibration period, incorporating six forces shaping the community [33]. 411 412 Predictions of community change for the three pollution reduction scenarios are made and converted 413 into change in the CTI by using the STIs. The difference between predicted CTIs and observed 414 temperature quantifies the credits (equivalent to 0.1–0.6°C of cooling), completing the present-day 415 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 416 417 debt (0.8°C). Updated predictions for the pollutant reductions, in light of warmer environmental

418 temperatures, are then made (or for new interventions), leading to new credit estimates (0.1-0.5°C of
419 cooling) and completing the future climate budget.

420

#### 421 Figure 3. Basic accounting with climatic credits, debts and altered repayment rates. (A) 422 Climatic debt, D, accumulates as the observed temperature ( $T_{obs}$ ; solid red line) increases more 423 rapidly than the reconstructed temperature ( $T_{rec}$ , solid black line). At the start of the period, the 424 community is in equilibrium with the environment (overlapping lines). The debt is estimated at time t 425 $(D_t)$ after which measures are implemented to pay part of the debt with climatic credit (solid blue 426 shading) and change the repayment rate (red and blue hatching). Climatic credit moves the 427 equilibrium temperature ( $T_{eqm}$ ; solid orange line) to a lower value than $T_{obs}$ , whilst the repayment rate 428 can be increased or decreased, leading to smaller (blue hatching; $T_{r2}$ ) or larger (red hatching; $T_{r3}$ ) 429 debt by $t_1$ respectively ( $D_{t1}$ ). $T_{rec}$ is the endpoint at $t_1$ assuming a 'business as usual' scenario. (**B**) A 430 hypothetical climate budget at t, comparing the estimated benefits of interventions for a river system. 431 The expansion of riparian shading and reduction of two stressors could accrue credit, whilst an 432 increase in water withdrawal would add further debt. Interventions could either increase the 433 repayment rate (e.g. removing barriers to increase connectivity) or decrease the rate (e.g. by 434 maintaining cool-water salmonid populations via regular re-stocking), leading to smaller or larger 435 debts respectively. The effects of altered repayment rates are estimated for a fixed time period (e.g. 436 20 or 50 years), allowing a rate to be converted to °C. 437 438

## 439 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.

443

#### 446 **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].

453

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).

459

460 Prober et al. [45] split climate change adaptations into four, reflecting quadrants based on 461 two axes (Fig I): i) interventions to 'evade or ameliorate' climate effects versus developing 462 the adaptive capacity of ecosystems; and ii) conservative, 'low regrets' options versus more proactive and potentially risky 'climate targeted options'. Many credit options gualify as low 463 regrets and aim either to ameliorate rising temperatures (e.g. restoring riparian tree cover for 464 465 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 466 467 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 468 microclimates and create refugia [15], or planting non-native trees to cast deeper shade in 469 forests [58]. 470

471

472 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 473 474 [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 475 476 undesirable state. Options for reducing the repayment rate qualify as low regrets in the short 477 term, acting to ameliorate rising temperatures, but failure to adapt may be higher risk in the 478 long term. An example of this approach is augmenting existing populations of cooler-climate 479 species to prevent local extinctions [45]). In practice, such repayment rate reductions might 480 be combined with credit options (e.g. encouraging denser tree canopy cover [9]), to minimise change whilst the credit option is fully implemented. 481

482

483

#### 484 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<sup>-1</sup>). 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

- 499 present, the inferred temperature will be lower than the observed temperature. Also500 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<sup>-1</sup>). The inverse of the relaxation time.
- **Resistance** the extent to which a community changes in response to a perturbation.

512 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.
- 515
- 516











530 **Fig I.** 

531

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

Build adaptive capacity

532