Challenges to natural and human communities from surprising ocean temperatures

Andrew J. Pershing[a,1], Nicholas R. Record[b], Bradley S. Franklin[a,c], Brian T. Kennedy[a], Loren McClenachan[d], Katherine E. Mills[a], James D. Scott[e,f], Andrew C. Thomas[g], and Nicholas H. Wolff[h]

[a]Gulf of Maine Research Institute, Portland, ME 04101; [b]Bigelow Laboratory for Ocean Sciences, East Boothbay, ME 04544; [c]School of Public Policy, University of California, Riverside, CA 92521; [d]Department of Environmental Studies, Colby College, Waterville, ME 04901; [e]Cooperative Institute for Research in Environmental Sciences, University of Colorado Boulder, Boulder, CO 80309; [f]Physical Sciences Division, National Oceanic and Atmospheric Administration Earth System Research Laboratory, Boulder, CO 80305; [g]School of Marine Sciences, University of Maine, Orono, ME 04469; and [h]Global Science, The Nature Conservancy, Brunswick, ME 04011

The community of species, human institutions, and human activities at a given location have been shaped by historical conditions (both mean and variability) at that location. Anthropogenic climate change is now adding strong trends on top of existing natural variability. These trends elevate the frequency of "surprises"—conditions that are unexpected based on recent history. Here, we show that the frequency of surprising ocean temperatures has increased even faster than expected based on recent temperature trends. Using a simple model of human adaptation, we show that these surprises will increasingly challenge natural modes of adaptation that rely on historical experience. We also show that warming rates are likely to shift natural communities toward generalist species, reducing their productivity and diversity. Our work demonstrates increasing benefits for individuals and institutions from betting that trends will continue, but this strategy represents a radical shift that will be difficult for many to make.

climate change | climate impacts | adaptation | warming | oceans

The communities of species at any point on the globe have traits that allow them to survive and reproduce in the predominant conditions. The characteristics of nearby human communities also reflect the regional climate. The adjustment of human organizations to prevailing climate conditions has happened over many generations. Much of this adjustment represents "reactive adaptation," meaning that responses are motivated and guided by past events (1–3). In many cases, adaptation to environmental conditions takes the form of problem solving, where change is made to reduce the impacts of a recently observed stressor (4).

Implicit in the natural, backward-looking approach is the expectation that past conditions provide insights to future conditions. We are rapidly moving into a world where this assumption will no longer apply. We know that the climate is changing, and there is growing certainty over the magnitude of change at both the global and regional levels (5, 6). We know that ecosystems and humans will adjust to these conditions, but we do not know the rate of environmental change above which these natural processes of adaptation will become insufficient to maintain key functions.

A corollary to the assumption that natural and human systems have adjusted to historical conditions is that conditions that fall outside of the range of experience have a high potential to drive change in the system, including evolutionary adaptation (7). In the oceans, recent marine heat waves have led to unexpected impacts in the natural communities and the human communities connected to them. The 2012 North Atlantic heat wave caused the catch of lobsters in the United States and Canada to spike a month earlier than normal, creating a market glut and collapse in price (8). The Pacific Blob event caused a harmful algal bloom that prompted managers to close the Dungeness crab fishery (9). These dramatic events often motivate changes in the human system that make it more adaptive and hopefully resilient to future changes. For example, after 2012, the Maine lobster industry added processing capacity and invested in marketing. These changes helped the fishery to achieve record value in 2016 despite near-record warm conditions (3).

Because of thermal inertia, temperature variability in the ocean is lower than in the atmosphere, making trends more apparent and increasing the rate at which new climates emerge (10–12). Using ocean ecosystems as a model, we develop a theory that encompasses how both natural and human systems respond to climate trends and variability. Natural systems and the human systems that are coupled to them have traits that determine their success under different environmental conditions. Our theory builds from the assumption that the distribution of these traits has been shaped by historical environmental variability to be close to optimal in the current environment. In other words, the system has adapted to the mean conditions and characteristic variability. Our goal is to characterize how systems that have adapted in this way will respond to trends.

Results

We begin by considering the frequency of unlikely events—"surprises"—that have the potential to challenge both natural and human systems. We define a temperature surprise as an annual mean temperature that is 2 SDs above the mean, where

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Significance

Based on historical and lived experience, people expect certain conditions to prevail in the ecosystems they depend upon. Climate change is now introducing strong trends that push conditions beyond historic levels. Using ocean ecosystems as a case study, we show that the frequency of surprising temperatures is increasing faster than expected. We then use these events as motivation to develop a theory for how temperature trends and events will impact natural and human communities. The theory suggests that strong trends will decrease the abundance and productivity of natural communities. Increasing trends will also challenge how people make decisions, and our theory identifies the conditions under which there is a significant payoff for people to bet on the trend.

the mean and SD are determined by the prior 30 y. This rolling-mean approach embeds a simple notion of adaptation and assumes that natural or human communities adjust to reflect prevailing conditions. If the environment were stationary (constant mean and variance), then the probability of encountering a surprising temperature would be 0.023 (assuming a normal distribution). The presence of a trend increases P_s—the probability that an agent that forms its expectations using the rolling mean encounters a surprise (*Methods*).

The frequency of surprising temperatures in 65 large marine ecosystems (LMEs) varied throughout the 20th century (Fig. 1*A*). Before 1940, it was rare for more than 3 LMEs to experience a surprise in the same year. A brief warming period during the 1940s led to an increase in the number of surprised regions. For much of the record, the number of surprised regions closely tracks the expectations based on the probability of surprise assuming the trend (P_s), although 2 years, 1941 and 1942, saw an exceptionally large number of surprised LMEs. The number of surprised LMEs declined after 1945 and remained low through the early 1980s. Then, as global warming accelerated, the observed and expected number of surprised LMEs began to increase. The number of years with many more surprises than expected increased dramatically after 1998. That year followed the powerful 1997/1998 El Niño. The exceptional number of temperature surprises in 2010 and 2016 also occurred following El Niño conditions. The number of cold surprises (Fig. 1*B*) has declined during the recent warming period, and only 4 cold surprises have occurred since 2000.

The past variability and the recent increase in surprises was not uniform across the globe. In most regions, the difference between the number of surprises and the number expected based on the local trends and variances increased suddenly in 1998 (Fig. 2*A*). The number of these "surprising surprises" continued increasing in the Arctic and North Atlantic. The Indian Ocean and Pacific regions leveled off then began increasing in 2010. Between 1999 and 2018, there were many more regions with more surprising temperature events than expected (48 of 65; Fig. 2*B*).

The formula for P_s accounts for steady changes in temperature over a sliding reference period. Accelerating warming would lead to an increase in the frequency of surprises above what the simple linear theory predicts. For each LME, we compared the warming rate and interannual variability over the period 1986 to 2000 with those from the period 2004 to 2018 (i.e., representing conditions at the beginning and end of the recent 30-y period). A linear model built with the difference in the warming rate and the difference in the variability explains 35% of the variability in the number of surprising surprises ($R^2 = 0.35$, $P < 0.001$) during the last 20 y (Fig. 2*C* and *SI Appendix*, Table S2).
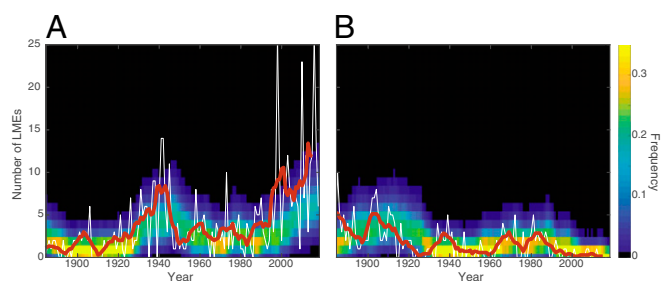
At a given level of interannual variability, there is a warming trend that gives the maximum probability of surprise. As the characteristic variability in the environment increases, the trend that produces the maximum also increases (Fig. 2*D*, gray contours). The average LME now has a probability of surprise of 11% (black star), but there are many regions (blue dots) with probabilities approaching the maximum level. The current distribution of trends and variance is similar to climate projections (RCP8.5; *Methods*) for 2030 (blue square). By 2060, the increase in the warming trends will push the average probability of surprise to 0.15 (purple square) with a large portion of the LMEs falling close to the theoretical maximum. Only a slight increase in the average probability of surprise occurs over the subsequent 30 y (red square and ellipse).

Our analysis suggests that the frequency of surprising temperature events in the oceans has increased and will continue to rise. These events have the potential to disrupt both ecosystems and human systems that are coupled to them. However, neither natural nor human systems are static. Both systems will respond to changes and have the capacity to adjust to prevailing conditions. The question is how will these systems respond to the trends that are beginning to dominate across the globe? To answer this question, we developed simple models of both a natural and human system that have adjusted to a specific level of temperature variability and then evaluate how they respond to a trend.

Our definition of a surprise contrasts the difference between reality and expectations formed assuming an environment with a constant mean and variance. Building from this concept, we created a simple model to represent a richer array of interactions between human expectations and environmental conditions. This model gives the human agents a payoff when environmental conditions fall within expectations, and conversely, they incur a loss when surprised. We describe this model using economic terms (investment, revenue, etc.), but the model is meant to encompass a wider range of interactions with the environment. For example, the investment in a particular range of conditions could represent an economic activity such as a fisherman investing in permits, and gear to catch fish that are abundant in a range of temperatures or it could represent management actions such as the allocation of fishing quota or a fishery closure that produce conservation benefits under a defined range of conditions.

We begin with an economic agent who makes investments across a range of temperatures, essentially betting on what ecosystem conditions will occur in the next year. The agent is assumed to be risk-neutral and can either concentrate its investments around a central temperature and receive a large potential payoff (or large potential loss) or it can spread its investments across a range of temperatures but receive a reduced return. If the environment is steady with a prescribed variance, then there is a strategy (temperature range) that produces the optimal average rate of return.

Unlike species that either move or die in response to unfavorable conditions, humans have the potential to change their strategies. This change could either reflect past conditions (backward looking) or it could incorporate a projection of future conditions (forward looking). For the backward-looking strategy, agents examine the recent 30 y, estimate the mean and variance, and adjust their investments assuming the environment will exhibit the same mean and variance over the next 30 y. This corresponds to the assumption that any trend is part of a natural cycle that could reverse at any time. Agents using the forward-looking strategy compute a linear trend from the last 30 y of data and adjust their strategy to maximize discounted returns over the next 30 y under the assumption that the trend continues.

The performance of the backward-looking strategy declines as the magnitude of the trend increases (Fig. 3*A*). However, the backward-looking strategy interprets very large trends as enhanced variability, and revenue rebounds slightly. If the ecosystem has higher

Fig. 1. Frequency of surprising ocean temperatures. (*A*) Number of LMEs (annual, white; 5-y smoothed, red) with an annual temperature 2 SDs above the mean of the previous 30 y. The shading indicates the probability of a specific number of surprises in each year after accounting for the trend. (*B*) Same but for cold events.

Fig. 2. Frequency and spatial pattern of surprising ocean temperatures. (*A*) The difference between the observed and expected number of surprises in 20-y windows plotted by regions (*SI Appendix,* Fig. S1). (*B*) The observed minus expected surprises between 1997 and 2018 for the LMEs and the open ocean (LME names defined in *SI Appendix,* Table S1). (*C*) Observed and expected surprises modeled as a function of the change in trend and in variance ($R^2 = 0.35$, $P < 0.01$). (*D*) The mean temperature trend and variability of the LMEs in 2018 (black star with 75% ellipse) and projected for 2030, 2060, and 2090 (blue, purple, and red squares, respectively). Individual LMEs in 2018 are shown (circles). Note that the 2 LMEs with slightly negative trends, Humboldt Current ($r = -0.006$, $\gamma = 0.38$) and Patagonian Shelf ($r = -0.004$, $\gamma = 0.28$), are not shown.

interannual variability, the agent will be spreading its investments over a wider range of temperatures and its revenue declines more gradually as the trend increases. Conditions that produce a high likelihood of a surprise lead to poor performance of the backward-looking strategy. This correspondence is not unexpected given that the definition of a surprise is so similar to the calculations that underlie the backward-looking strategy.

Revenues decline with increased warming for firms using the forward-looking strategy (Fig. 3*B*), but the decline is less severe. The backward-looking strategy is only able to outperform the forward-looking strategy if the trend is weak and/or if the interannual variability is very high. As configured, the forward-looking strategy becomes more profitable when the probability of surprise exceeds 7%. All but 12 of the 65 LMEs have already exceeded this threshold.

Thermal responses describe a substantial component of marine species distributions and diversity (13), although the responses are often nonlinear and sensitive to variance (14). Rather than attempt to reproduce the dynamics of a particular ecosystem, we developed an idealized model of a community that has adjusted to a specific level of temperature variability. We begin with a community of species that are competing within an environment where temperature is the constraining environmental variable. Each species has a thermal niche defined by 2 traits, the preferred temperature (t_j) and a parameter β_j that determines how quickly its growth rate declines as conditions become less favorable—i.e., the niche breadth. We assume that the species have evolved together in an environment with no temperature trend and constant variability. This assumption implies that species with the same preferred temperature have the same long-term average growth rates when integrated over historical variance, regardless of their

niche breadths. We created a community of species that cover a range of preferred temperature and temperature tolerances—a trait space. We then allowed that community to reach an equilibrium under temperatures that vary around a stable mean.

After the adjustment period, only species with a temperature preference close to the mean are successful in this environment and abundance does not vary substantially with β, the temperature tolerance (Fig. 4*A*, community with doubling time of 1 y and interannual variability of $\gamma = 0.3°$). Exposing this community to a 100-y warming trend similar to the recent global ocean average ($r = 0.02°·y^{-1}$), increases the growth rate of species with higher thermal preferences, and the distribution of species shifts to the

Fig. 3. Performance of the 2 human–system adaptation strategies. (*A*) Net revenue of backward-looking strategy with moderate switching cost ($c = 10$). The net revenue in each row (value of interannual variability) is normalized by the revenue when there is no trend. (*B*) Same as *A* but for the forward-looking strategy. The ellipses contain 75% of the LMEs in 2018 (solid ellipse, star) and in 2090 under RCP8.5 (dashed ellipse, square).

right in trait-space (Fig. 4*B*). However, the peak lags slightly behind the actual temperature (dashed line) and the total abundance decreases. The decline in abundance is strongest for species with narrow temperature tolerances, while species with wider temperature tolerances begin to grow sooner and persist longer than the more specialized species. This causes the trait-space distribution to shift up (i.e., toward generalists). Doubling the warming rate ($r = 0.04°·y^{-1}$) intensifies the decline in abundance, the shift toward generalists, and the lag between the mean temperature preference and the mean temperature (Fig. 4*C*). For a given level of interannual variability (γ; rows in Fig. 4 *D* and *E*), increasing the warming rate increases the relative fitness of the generalist strategies. This results in a decline in the total abundance of the community. The decline in abundance with increasing warming trend occurs at all levels of interannual variability, but higher interannual variability reduces the rate of decline (Fig. 4*D*).

Total abundance is important, for example, as an indicator of potential fishery yields. However, the way biomass is distributed among species is also important. We characterized the change in the shape of the distribution using the Shannon diversity index (15). This is an index of how smoothly biomass is spread across the trait space (higher values indicate similar abundances of all species, i.e., high biodiversity). In this model ecosystem, an increasing warming rate causes diversity to initially decline (Fig. 4*E*). This is a result of the increased fitness of species with wider temperature tolerances (the upward shift in trait-space in Fig. 4*B*). However, at higher warming rates, diversity increases as species whose growth rates and abundances are increasing overlap with species no longer at their optima (i.e., the "tail" in Fig. 4*C*). For a community with a shorter doubling time, the community translates more smoothly in trait-space, and the shift from reduced to enhanced diversity occurs at lower warming rates (*SI Appendix,* Fig. S4). While surprising events have an impact on our modeled biological communities, surprises, as we define them, are not driving the overall pattern. Natural communities integrate conditions over many years, making the absolute warming rate more important.

Discussion

According to our analysis, marine ecosystems are experiencing more frequent surprises, even accounting for recent warming

trends. Our model of natural communities suggests that this will result in a decline in the abundance of species occupying a similar trophic niche; however, the decline will be less strongly felt by fast-reproducing species. This creates the potential for decoupling between different components of the food web. For example, some gelatinous zooplankton can double their abundance in a few days. While the species composition in a region will change, the fast-reproducing component of the ecosystem is more likely to maintain high biomass levels than slower-reproducing species such as fish. If they are trophically coupled, reducing the slower-growing predators will further increase the abundance of the faster-growing prey. Adding additional processes such as immigration and dispersal could alter these effects, potentially providing a way for the dynamics in the slow-reproducing community to get closer to those in the faster community.

Although this model was not designed to replicate a particular community, the responses of the idealized communities to warming have parallels to changes in coral reef ecosystems. Corals with the narrowest thermal range also tend to have higher growth rates, similar to the specialist–generalist trade-off embedded in our neutral model. Warming and associated bleaching events are causing a shift to slower-growing species with wider thermal tolerances as well as lower structural complexity (16, 17). The long-term warming in the tropics is contributing to a decline in coral cover (18, 19), consistent with our prediction of reduced abundance. The shifts toward lower coral cover and less complex reefs have important ramifications for the ecosystem services reefs provide (20), including fisheries (21, 22) and shoreline protection (23, 24).

For the human system, the lesson is clear: Historical experience is becoming less relevant. To be successful, human institutions including businesses, communities, management agencies, and governments will need to adopt strategies that look forward rather than backward. For example, when the Gulf of Maine experienced a rapid increase in temperature, the backward-facing fishery management process was not able to act quickly enough to reduce fishing on cod and avoid a collapse of the fishery (25).

Scientists have developed a range of forecast products that could support forward-looking decisions. Climate models provide a long-term view and express contingencies related to global carbon emissions (26). Seasonal and multiyear forecasts are becoming more established (27), although the timescale at which these are reliable changes from region to region (28). Our results strongly suggest that betting on the status quo will be an increasingly risky strategy. Financial tools such as insurance or derivatives can provide a way for individuals or companies to buffer loses (29).

While we have the tools to shift to forward-looking decision making, it is not clear how quickly or even whether we will make this shift. Humans are naturally resistant to change and institutions tend to be conservative (30, 31). Shifting to a forward-looking strategy is risky, and it is reasonable for managers, politicians, and CEOs to expect that they will be punished more severely for the failure of a new strategy than poor performance of a traditional one (32). Broad societal acceptance of the realities of climate change trends and the reliability of climate projections is a critical prerequisite to forward-looking adaptive action. However, experience is the most valuable teacher. It will likely take more experience with extreme events before people decide to stop being surprised by them.
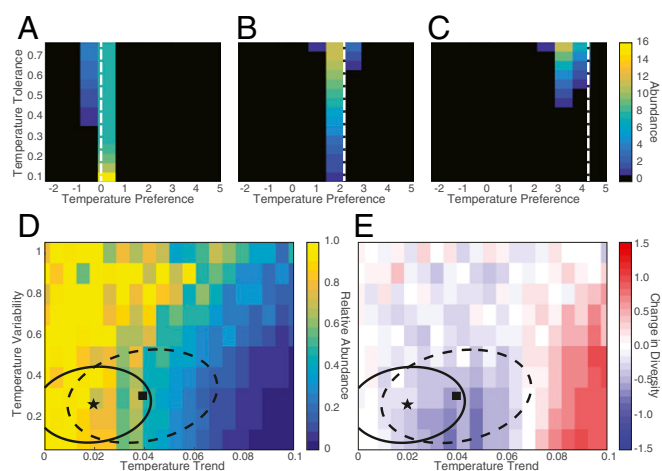

Fig. 4. Dynamics of a neutral community model under warming trends. Abundance of species across trait space (preferred temperature and temperature tolerance) at the start of the warming period (*A*) and after 100 y of warming with a rate of $0.02°·y^{-1}$ (*B*) and $0.04°·y^{-1}$ (*C*). The dashed white lines in *A–C* are the mean temperature. (*D*) Total abundance (proportion of the abundance before warming) as a function of warming trend and interannual variability. (*E*) Change in community diversity between the start and end of the warming period. Ellipses contain 75% of the LMEs as in Fig. 3.

Methods

Ocean Temperature Data. We used sea surface temperature (SST) data from version 4 of the Extended Reconstruction Sea Surface Temperature (ERSST) dataset of the National Oceanic and Atmospheric Administration (NOAA) (33). This dataset consists of monthly mean SST at 2°-by-2° resolution from 1854 to present. Data through the end of 2018 were included in this analysis. We produced SST anomalies relative to the 1982 to 2011 average. We then

averaged the monthly anomalies over each year to produce annual SST anomalies.

We further partitioned the data into the standard LMEs defined by NOAA (34) (*SI Appendix*, Table S1 and Fig. S1) and computed the average temperature for each LME. Note that we did not include the Southern Ocean in our analysis due to missing data before 1950.

To examine future temperature variability and trends, we computed annual averages over the 65 LMEs for 27 models in the CMIP5 climate model integration using RCP 8.5 (35). Our analysis of the climate model output focuses on the variance and the trend. These statistics do not depend on the mean of the data (it is removed in the calculation), so there is no need to correct the mean bias in the climate model output.

Ocean Temperature Surprises. We define a surprise as an event with conditions that exceed expectations based on recent history. While we will focus on annual temperatures, this definition can be applied broadly to other physical, chemical, biological, ecological, and socioeconomic conditions. $T(j)$, the temperature in year j is a "surprise" if $T(j)$ is greater than a critical temperature T_s. We define T_s as the solution to the following:

$$Z(T_s, [T(j-n), T(j-n+1), \ldots, T(j-1)]) = (1-p), \qquad [1]$$

where Z is the cumulative probability distribution of T estimated using the n prior years of data and p is a probability threshold. Note that if $T(j)$ qualifies as a surprise, then it will reduce the chance of the next year being surprising as it will increase the mean and variance of the distribution estimated in the next year.

To determine whether the frequency of surprises is itself surprising, we developed a simple statistical model of surprising events. We assume that mean conditions increase linearly over the reference period at rate r. Furthermore, we assume that the temperature in a given year is normally distributed about the mean conditions with a constant variance of (γ^2). It is straightforward to show that the mean over the reference period is $rn/2$. We used a Monte Carlo procedure to explore how the interannual variance, trend, and time series length interact to determine the variance over the entire reference period (σ^2). We found that the following equation:

$$\sigma^2 = \frac{2n-1}{2n}\gamma^2 + \frac{1}{12}(n^2 + n - 7)r^2, \qquad [2]$$

accurately captures the relationship among these variables. Using the cumulative normal distribution $\Phi(T \mid rn/2, \gamma)$ in place of Z above, the probability of a surprising event (P_s) is $1 - \Phi(T_s, r(n+1), \gamma)$. We calculated the statistics t_0, σ, r, and γ for rolling 30-y periods for each ERSST cell and each LME region in the ERSST and CMIP5 data. We then computed P_s for each year using the statistics from the previous 30 y.

Environmental Model. Globally, temperature (T) is the most important indicator of environmental conditions. Thus, we couch our economic and ecological modeling below in terms of temperature, although the frameworks are general. For the experiments for each model, we envision an ecosystem with a historical mean temperature of T_0 and interannual SD γ. We assume that the economic or ecological conditions have equilibrated to this environment. Then, we introduce a warming trend r. For simplicity, we did not consider autocorrelation in the forcing time series.

To simulate this environment, we drew normally distributed random variables from a distribution with mean = T_0 and SD = γ during an initial equilibration period. We then impose a trend by adding rj to the mean, where j is the time after the trend begins. Trends ranged from 0 to 0.1 °C y^{-1}. Temperature variability ranged from 0.1 to 1 °C.

Economic Model. We imagine an economic agent that makes a series of investments that align with a particular temperature. The revenue received in a year depends on the temperature (T_j) and how much has been invested. We model the investment return as a function:

$$R(T_j \mid t_j, \beta_j) = N(T_j \mid t_j, \beta_j) - N(t_j + 2\beta_j \mid t_j, \beta_j), \qquad [3]$$

where $N(\bullet)$ is the normal distribution function. The function is controlled by 2 parameters, a central temperature t_j and a parameter β_j that governs the spread of temperatures where returns are possible. As β_j increases, the width of the area where positive returns are possible increases in exchange for a decrease in the maximum payoff. Note that $R(t)$ is a normal distribution function shifted downward so that it is positive in the range $t_j \pm 2\beta_j$.

We allow the agent to change its investments (adjust t_j, β_j) from year to year, based on information about the environment. However, we impose a cost for changing strategies, based on the difference between the new and old distributions:

$$C(t_j, \beta_j, t_k, \beta_k) = c \int_{-\infty}^{\infty} \left(N(T \mid t_j, \beta_j) - N(T \mid t_k, \beta_k) \right)^2 dT$$
$$= c \int_{-\infty}^{\infty} \left(N_j^2 + N_k^2 - 2N_j N_k \right) dT, \qquad [4]$$

where c is a positive number.

In each year, we imagine that the agent can look at the previous M years of temperature data and adjust t_j and β_j. Let $N(T \mid T_{est}, \gamma_{est})$ (normal distribution with mean = T_{est}, and SD = γ_{est}) be the estimate made by the agent of the likely distribution of temperatures in the year in question. With this function, we can define the expected returns (dropping subscripts):

$$E(t, \beta, T, \gamma) = \int_{-\infty}^{\infty} R(s \mid t, \beta)N(s \mid T, \gamma)ds$$
$$= \int_{-\infty}^{\infty} N(s \mid t, \beta)N(s \mid T, \gamma)dT - \int_{-\infty}^{\infty} N(t+2\beta \mid t, \beta)N(s \mid T, \gamma)dT \qquad [5]$$
$$= \frac{1}{\sqrt{2\pi(\beta^2 + \gamma^2)}}e^{-(t-T)^2/(2(\beta^2+\gamma^2))} - \frac{1}{\sqrt{2\pi\beta^2}}e^{-2}.$$

Given an agent's perception of the environmental conditions (T_{est}, $_{est}$) and its current investments (t_{j-1}, β_{j-1}), its optimal investment strategy is defined by the values of t_j and β_j that maximize the discounted returns over the next M years:

$$\sum_{k=1}^{M} (1-d)^{-k} \left(E(t_j, \beta_j, T_{j+k}, \gamma_{j+k}) - C(t_j, \beta_j, T_{j+k}, \gamma_{j+k}) \right). \qquad [6]$$

The solution to [6] depends critically on how the agent evaluates the state of the environment and estimates future conditions. We allow the agent to access the vector of temperatures from the N previous years: $\mathbf{T} = [T_{j-N}, T_{j-N+1}, \ldots, T_{j-1}]$. The algorithm to estimate the environment forms a strategy. We consider 2 strategies. The natural or backward-looking strategy computes the mean and variance from $\mathbf{T}$ and assumes that these conditions will persist. The alternative strategy is to use linear regression to estimate the temperature trend and interannual variance as in [2]. Under this forward-looking strategy, agents assume that the trend will persist and optimize accordingly.

We evaluated the performance of the different adaptation strategies under different environmental and economic conditions. The economic conditions are specified by the cost of switching (c), and we tested costs of 0, 1, 10, and 100. The environmental conditions were specified by the trend and the interannual variance as described above. We then applied the natural or trend algorithm with $n = 30$.

For each simulation (36), we randomly generated a time series of 130 y. Agents were given 30 y of temperature data. They applied their algorithm to evaluate the state of the environment. They then inferred the investment strategy that would maximize the perceived value of their investments under their perception of the future environment. Agents optimized their investments using a discount rate of $d = 0.03$ and a time horizon of $M = 30$ y. We compared strategies by the sum of their net revenue over the 100 simulated years.

Ecosystem Model. We imagine a community of species that are competing within an environment where temperature is the only environmental conditions. A species is defined by 2 traits, the preferred temperature (t) and a parameter β that determines how quickly its fitness declines as conditions become less favorable. In an environment with variance γ^2, the population growth rate of species j is as follows:

$$G_j(T \mid t_j, \beta_j) = g(\beta_j, \gamma)N(T \mid t_j, \beta_j), \qquad [7]$$

where

$$g(\beta, \gamma) = \frac{\ln(2)}{D}\left(\int_{-\infty}^{\infty} N(T \mid 0, \beta)N(T \mid 0,)dT \right)^{-1}, \qquad [8]$$

and where D is the time for the population to double at the preferred temperature. The function g ensures that species with the same t have the

same fitness (expected value of G in the environment) even if they have different values of β.

We represent interactions among the species using a modified logistic equation (37):

$$\frac{dS_j}{dt} = G_j(T)S_j - \mu S_j^{1+\phi} S_{tot}^{1-\phi},$$ [9]

where S_j is the abundance of species j and S_{tot} is the total abundance of all species. The parameter ϕ controls the degree to which the species interact. If $\phi = 1$, then S_{tot} is eliminated [9], becomes the standard logistic equation, and each species will approach the same carrying capacity of G^*/μ (where G^* is the time-averaged growth rate). If $\phi = 0$, then the species are tightly linked, and the species with the fastest growth rate will outcompete the others. Because G^* is the same for all species, competitive exclusion is prevented in the long term in an environment with constant mean and variance.

The parameters t_j and β_j define a particular strategy. Species with small β_j specialize at a narrow range of temperatures, while generalists have large β_j and are moderately successful across a wider range of temperatures (although because of g, both have the same long-run fitness in a steady environment). We explored how the fitness of these different strategies changes as an ecosystem experiences a warming trend (36). First, we defined 300 species by crossing 20 evenly spaced values of t between −2 and 12 and 15 values of β between 0.1 and 0.75. We initialized the community with the density of each species set to 0.001. We then specified the dynamics of the community. This is set by the population doubling time (D) and the

coexistence parameter ϕ. We tested $D = 0.5$, 1, 2, and 4 y, and $\phi = 0.25$, 0.5, 0.75, or 1.

For each community, we selected a value of inherent variability (γ) and integrated [9] for 500 y. This allowed the population to reach a quasi-steady state. Then, we exposed the community to a steady warming trend, integrating over the next 100 y. We compared the total abundance and diversity over the last 20 y of the spin-up period and the last 20 y of the warming period. We used the Shannon index:

$$H = -\sum_{j=1}^{n} S_j' \log S_j',$$ [10]

as our index of diversity where S_j' is the abundance of species j expressed as a proportion.

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