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Ecosystem Service Supply and Vulnerability to Global Change in Europe

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5. Supporting Online Material is available on *Science* Online.
6. All transcriptional reporters were made by polymerase chain reaction (PCR) fusion, from the predicted start to the next predicted upstream gene, and extrachromosomal arrays were marked with *pha-1(+)*. Expression of *mir-61* transcription was studied by using the *arIs107* integrant, which displayed the same pattern as extrachromosomal arrays.
7. *mir-61* is also expressed in cells of the somatic gonad in which LIN-12 is active, and this expression is also lost when the LBSs are mutated (Fig. 1, B and C). In contrast, expression in other tissues where we have no evidence that *lin-12* activity is functionally relevant, such as intestinal cells, is unaffected. These observations suggest that the loss of expression in P5.p and P7.p reflects lack of response to *lin-12* and not loss of a general enhancer.
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Ecosystem Service Supply and Vulnerability to Global Change in Europe

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Global change will alter the supply of ecosystem services that are vital for human well-being. To investigate ecosystem service supply during the 21st century, we used a range of ecosystem models and scenarios of climate and land-use change to conduct a Europe-wide assessment. Large changes in climate and land use typically resulted in large changes in ecosystem service supply. Some of these trends may be positive (for example, increases in forest area and productivity) or offer opportunities (for example, "surplus land" for agricultural extensification and bioenergy production). However, many changes increase vulnerability as a result of a decreasing supply of ecosystem services (for example, declining soil fertility, declining water availability, increasing risk of forest fires), especially in the Mediterranean and mountain regions.

To sustain a future in which the Earth's life-support systems are maintained and human needs are met, human activities must first be recognized as an integral component of ecosystems (*1*, *2*). Scenarios of global change raise concern about alterations in ecosystem services such as food production and water supply, but the potential trajectories of change, especially at the regional scale, are poorly characterized (*3*). We investigated the changing supply of ecosystem services in a spatially explicit vulnerability assessment of Europe, using multiple global change scenarios and a set of ecosystem models. A dialogue with stakeholders from relevant sectors was conducted throughout the study (*4*).

Our assessment was based on multiple scenarios for major global change drivers (socioeconomic factors, atmospheric greenhouse gas concentrations, climate factors, and land use). The scenarios were quantified for Europe (15 pre-2004 European Union members, plus Norway and Switzerland, henceforth referred to as EU15+) during the 21st century at 10′-by-10′ latitude/longitude grid resolution, and for periods ending in 2020, 2050, and 2080, relative to baseline conditions in 1990 (*5*). Socioeconomic trends were developed from the global Intergovernmental Panel on Climate Change Special Report on Emission Scenarios (IPCC SRES) storylines B1, B2, A1FI, and A2 for EU15+ (*4*, *6*, *7*) (table S1). With this common starting point, socioeconomic changes relate directly to climatic changes through greenhouse gas concentrations and to land-use changes through climatic and socioeconomic drivers, such as demand for food. Four general circulation models (GCMs)—the Hadley Centre Coupled Model Version 3 (HadCM3), the National Center for Atmospheric Research–Parallel Climate Model (NCAR-PCM), the Second Generation

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Coupled Global Climate Model (CGCM2), and the Commonwealth Scientific and Industrial Research Organisation–Climate Model Version 2 (CSIRO2)—were used to simulate climatic changes (*4*). Out of 16 combinations of storylines and GCMs, we selected seven scenarios for interpretation: B1, B2, A1FI, A2 calculated with HadCM3 (variation across storylines, "socioeconomic options"), and A2 calculated additionally with three other GCMs (variation across climate models, "climatic uncertainty") (Table 1) (*4*).

Temperature-change scenarios in Europe vary regionally but show a clear trend toward warming. The average projected temperature increase in Europe ranged from 2.1° to 4.4°C (across storylines) and from 2.7° to 3.4°C for the A2 storyline (across GCMs) (Table 1), with the strongest warming consistently in the high latitudes (fig. S1). Seasonal and regional variation of changes in precipitation was considerable. Generally, all scenarios concurred on decreasing precipitation in the south of Europe, particularly in summer (Table 1), and increasing precipitation over much of northern Europe (fig. S2).

Land-use scenarios (*4*) showed little variation based solely upon different GCMs, indicating that socioeconomic assumptions had a greater effect on land use than did climatic drivers. The general trends were of reductions in agricultural areas for food production, partly compensated for by increases in bioenergy production and forests, as well as small increases in urban and protected areas (Table 2). In the A (economic) scenarios, the decline in agricultural land was especially pronounced (Fig. 1), mainly owing to assumptions about the role of technological development (*8*). The land that becomes "surplus" to the requirement of food production would allow balancing the production of other ecosystem services against food production, for example through extensification (*9*) or bioenergy production (*10*).

We next examined the changing supply of a number of ecosystem services owing to global change in Europe. The selected services reflect the availability of modeling tools adequate for pan-European assessment and the aim for a broad range of terrestrial services covering the four service categories identified by the Millennium Ecosystem Assessment (*1*).

The European Commission proposed a target of doubling the contribution of renewable energy sources to the EU's total primary energy needs to 12% by 2010 (*11*). Biomass energy will add to this goal. We assessed the potential distribution of 26 bioenergy crops under changing climatic conditions (*4*). The potential distribution of bioenergy crops increased in northern Europe as a result of increasing temperatures (Table 2). These potential gains are optimistic, given that restricting soil conditions are not taken into account. In contrast, the available choice of bioenergy crops decreased in southern Europe owing to increased drought, unless production systems are adapted (Table 2).

Changes in the provision of water affect humans directly and indirectly through effects on other ecosystem services. At the global scale, increases in population and consumption alone will reduce water availability (*3*, *12*, *13*). We quantified the implications of population and climate change on water availability in EU15+ using a macroscale hydrological model (*4*). In 1995, approximately 193 million people out of a total EU15+ population of 383 million lived under water stress (water availability <1700 m^3 capita^{-1} year^{-1}) (*14*). In the absence of climate change, these numbers decreased by 2080 where population decreased (scenario B2, Table 1). In contrast, population and climate change increased in the numbers of people living in water-stressed watersheds and exacerbated water deficiency for many already stressed areas (Table 2), particularly in southern Europe (Fig. 2). Under the A1FI, A2, and B1 scenarios, between 20 and 38% of the Mediterranean population would be living in watersheds with increased water stress (14% in B2). In this region, water scarcity would likely be aggravated by higher extractions per capita for irrigation and tourism (*15*).

Case studies for the Rhine, Rhône, and Danube basins, as well as for small Alpine catchments, indicated climate-induced changes in the timing of runoff (*4*). These result from impacts of rising temperatures on snow-cover dynamics, which enhanced winter runoff, reduced summer runoff (Table 2), and shifted monthly peak flows by up to two months earlier than at present (*16*). This reduced water supply at peak demand times and increased the risk of winter floods. Changes in snow-cover dynamics directly affect biodiversity at high elevations. Moreover, navigation and hydropower potential would be altered.

In addition to its importance for water supply and biodiversity conservation, snow cover is of course indispensable for winter tourism. The Alpine case studies indicated a rise in the elevation of reliable snow cover from about 1300 m today to 1500 to 1750 m at the end of

Table 1. Summary of the basic socioeconomic, atmospheric, and climatic drivers based on model outputs forced by SRES scenarios. Population and atmospheric CO_2 concentration estimates are for the year 2080. For the climatic indicators, 30-year averages 2051 to 2080 compared with 1961 to 1990 are shown. In this study, we focused on the HadCM3 climate model and the A2 storyline. The EU15+ population in 1990 was 376 million people. The GCMs were forced with these concentrations plus CO_2 equivalents accounting for the other greenhouse gases. The atmospheric CO_2 concentration in 1990 was 354 parts per million (ppm) by volume. Precipitation changes (%) on the Iberian Peninsula are given by season: JJA, summer (June, July, August); DJF, winter (December, January, February).

Scenarios by 2080	Climate model			
	HadCM3	NCAR-PCM	CGCM2	CSIRO2
	Storyline B1			
Population (10^6)	376	376	376	376
CO_2 concentration (ppm)	518	518	518	518
Δ Temperature (°C)	3.1	–	–	–
Δ Precipitation (%)				
Europe	4.8	–	–	–
Iberian Peninsula JJA	–17	–	–	–
Iberian Peninsula DJF	7	–	–	–
	Storyline B2			
Population (10^6)	346	346	346	346
CO_2 concentration (ppm)	567	567	567	567
Δ Temperature (°C)	2.1	–	–	–
Δ Precipitation (%)				
Europe	2.7	–	–	–
Iberian Peninsula JJA	–14	–	–	–
Iberian Peninsula DJF	7	–	–	–
	Storyline A1FI			
Population (10^6)	376	376	376	376
CO_2 concentration (ppm)	779	779	779	779
Δ Temperature (°C)	4.4	–	–	–
Δ Precipitation (%)				
Europe	–0.5	–	–	–
Iberian Peninsula JJA	–27	–	–	–
Iberian Peninsula DJF	2	–	–	–
	Storyline A2			
Population (10^6)	419	419	419	419
CO_2 concentration (ppm)	709	709	709	709
Δ Temperature (°C)	2.8	2.7	3.4	2.7
Δ Precipitation (%)				
Europe	0.5	2.3	0.0	–0.6
Iberian Peninsula JJA	–22	–18	–26	–19
Iberian Peninsula DJF	10	0	1	–3

Table 2. Summary of land-use drivers and global change impacts for Europe, time period 2080 compared with baseline (1990), unless otherwise noted (*4*).

Storyline	B1	B2	A1FI	A2	A2	A2	A2
GCM	HadCM3	HadCM3	HadCM3	HadCM3	NCAR-PCM	CGCM2	CSIRO2
Land-use model outputs forced by climate, CO_2, and interpretations of SRES storylines							
Land-use change (%)*							
Cropland (for food production)	–7.0	–6.4	–10.7	–10.4	–10.6	–10.7	–10.6
Grassland (for livestock)	–1.1	–6.7	–8.7	–10.0	–10.1	–10.2	–10.0
Forest	3.5	5.6	0.8	0.7	1.0	1.0	1.2
Urban	0.05	0.06	0.09	0.08	0.07	0.07	0.07
Bioenergy production	3.4	7.4	8.7	8.7	9.1	8.6	8.6
Protected	6.1	6.1	6.1	6.1	6.1	6.1	6.1
Surplus	1.1	0.0	9.8	10.9	10.5	11.2	10.8
Impacts as estimated by ecosystem models							
Δ Potential distribution of bioenergy crops (%)†							
Overall	3	4	1	3	6	7	5
Latitude 35 to 45	–7	–6	–13	–8	–1	–3	–2
Latitude 45 to 55	–1	0	–6	–2	4	8	–6
Latitude 55 to 65	12	13	12	13	11	14	15
Latitude 65 to 71	18	22	32	23	19	16	34
Additional people living under water stress (10^6)‡	44.3	25.8	44.3	15.7	7.5	11.7	5.8
People living under increased water stress (10^6)§	31.0	38.2	45.7	35.6	18.4	69.6	25.4
Δ Alpine summer runoff (%)‖	–24	-23	–46	–34	–12	–27	–20
Δ Elevation of reliable snow cover (m)‖	230	180	450	310	200	230	390
Species loss per grid cell (minimum to maximum %)¶	–7 to –58	–8 to –53	–8 to –59	–8 to –55			
Δ Area burnt, Iberian Peninsula (%)	112	57	80	55	–1	37	8
Δ Wood increment (%)	–10.0	9.7	3.8	4.4	2.9	2.9	6.2
Cumulative carbon balance (Pg C)#	2.2	2.4	1.8	3.0	4.9	4.1	3.7
Average carbon flux (% of emissions)**	2.5	2.7	2.1	3.5	5.5	4.7	4.2
Δ Soil organic carbon (Pg C)††							
Total	–0.1	–0.9	–4.1	–4.4	–4.3	–4.5	–4.8
Cropland	–4.3	–4.3	–5.9	–5.6	–5.4	–5.5	–5.8
Grassland	1.5	–1.2	–2.2	–2.7	–2.7	–2.7	–2.8
Forest	2.8	3.6	1.0	1.1	1.3	1.3	0.7

*Baseline areas (% of EU15+): Cropland, 23.0%; grassland, 17.2%; forest, 31.0%; urban, 1.5%; other (shrubland, barren land, wetland, inland waters, sea, permanent ice, and snow), 27.3%. For all scenarios, it is assumed that 20% of the area of Europe will become designated as "protected" by 2080. This was based on a judgment made from past and current increases in protected-areas coverage in Europe, the latter being due to member-state responses to the need for implementation of the NATURA 2000 network. Although this target was the same for all scenarios, it was assumed that it would be reached for different reasons: The economic scenarios require areas for recreation for a richer population, whereas the environmental scenarios require areas designated for conservation purposes (tables S1 and S2). "Surplus" is land that is left over when the demand for all land-use types is satisfied. †Change in potential distribution of 26 bioenergy crops (% land area) due to climate change. The estimates do not take soil conditions into account. ‡Additional people (millions) living in stressed watersheds due to climate change (compared with the hypothetical case of no climate change). Water-related resource problems are likely when water availability falls below the threshold of 1700 m^3 $capita^{-1}$ $year^{-1}$ (*14*). §People (millions) living in already water-stressed watersheds (less than 1700 m^3 $capita^{-1}$ $year^{-1}$), where climate change further reduces water availability by more than 10%. ‖Average of five Alpine case studies. ¶Year 2050 compared with the baseline (1990). The range of minimum (full instantaneous dispersal) to maximum (zero dispersal) loss is shown. Plants, mammals, reptiles, amphibians, and breeding birds were considered. This indicator records only losses from a specific grid cell and does not take potential gains into account. The indicator does not make a statement about potential losses of the species from Europe or about extinction. #Cumulative land-atmosphere carbon flux between 1990 and 2080. Positive values denote fluxes to land. **Average yearly land-atmosphere flux (1990 to 2080) relative to EU15+ CO_2 emissions in 1990. ††Change in cumulative soil organic carbon content in mineral soil down to a depth of 30 cm.

the 21st century (Table 2) (*16*). A 300-m rise of the snow line would reduce the proportion of Swiss ski areas with sufficient snow from currently about 85 to 63% (*17*).

Biodiversity is essential to ecosystem processes in ways that are not yet fully understood (*18*), and it is considered worth protecting in its own right (*3*). We used a statistical modeling framework to project the distribution of more than 2000 plant and animal species across Europe (*4*). These simulations do not incorporate effects of land-use change, because at the resolution of this study these were confounded with climate effects (*19*). We therefore present conservative estimates that neglect effects of habitat loss or landscape fragmentation (*20*). Projections of species loss per grid cell showed changes under all scenarios (Table 2). Mountains and Mediterranean species were disproportionately sensitive to climate change (fig. S3A) (*4*, *21*), in agreement with recent observations (*22*) and projections (*23*). Under the unrealistic assumption that all species can migrate instantaneously to newly suitable habitats, the relative potential gain of plant species in Mediterranean regions was relatively high because of habitat expansion (fig. S3B). However, unhindered expansion is unlikely because of the concurrent impacts of other drivers such as land use, nitrogen deposition, and biotic exchange, especially in the Mediterranean region (*20*). Flexible management of nature reserve areas may conserve species. However, stakeholders pointed out great difficulties in changing existing reserve boundaries under current policies and land-ownership restrictions.

To obtain more detailed results on tree species in the Mediterranean region, we used a process-based tree-growth model (*4*). The simulations corroborated negative effects on vegetation, especially over the long term, owing to increased drought. Furthermore, the area burnt by forest fires increased in this region under all but one scenario (*4*) (Table 2). The distribution of a number of typical tree species is likely to decrease in the Mediterranean region, such as cork oak (*Quercus suber*), holm oak (*Q. ilex*), aleppo pine (*Pinus halepensis*), and maritime pine (*P. pinaster*). These changes would have implications for the sense of place and cultural identity of the inhabitants, traditional forms of land use, and the tourism sector.

We assessed the potential impacts of management and global change on the overall wood production from European forest using an inventory-based model (*4*). In line with other industrialized areas, but opposed to global trends (*3*, *24*), the total European forest area was projected to increase (Table 2). Climate change resulted in increased forest growth (Table 2), especially in northern Europe. The impact of increased summer drought in southern Europe was partly mitigated by higher precipitation in spring and increased water-use efficiency in response to rising atmospheric CO_2 concentrations. Increasing forest area increased annual wood increment because of a high proportion of young stands. When low wood demand led to less intensive management (B scenarios), forests grew old and less productive, and increment decreased by 10.0% in the B1 scenario (in B2, afforestation counteracted this effect; Table 2). In general, management had a greater influence on wood production in Europe than climate or land-use change. As corroborated by stakeholders, forest management is influenced more strongly by actions outside the forest sector, such as trade and policies, than from within.

The total amount of carbon stored in terrestrial biosphere is an important factor in climate regulation (*25*). The net carbon land-atmosphere flux is determined by net primary production and carbon losses due to soil heterotrophic respiration, fire, harvesting, and land-use change. The aggregate land-atmosphere flux over Europe was estimated using a dynamic global vegetation model (*4*). Our results confirm that Europe's terrestrial biosphere currently acts as a net carbon sink (*26*) (Table 2). Land-use change affected this sink positively through decreases in agricultural land and increased afforestation. Furthermore, CO_2 fertilization enhanced net primary production. However, soil carbon losses due to warming balanced these effects by 2050 and led to carbon releases by the end of this century. The temperature effect on soil carbon losses is confirmed by recent experimental and modeling studies (*27*–*29*) and by separate calculations using a soil carbon model (*4*). Although afforestation led to a net increase in soil organic carbon in forest soils despite the losses due to warming, the total amount of carbon in European soils decreased (Table 2).

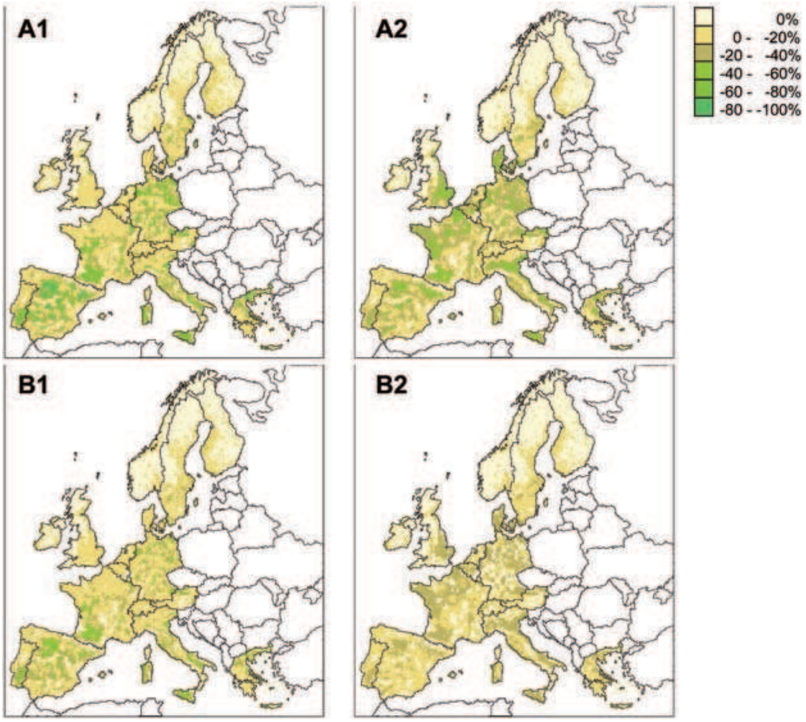

Fig. 1. Change in cropland area (for food production) by 2080 compared with the baseline (percentage of EU15+ area) for the four storylines [A1FI (A1), A2, B1, and B2] with climate calculated by HadCM3.

Stakeholders were primarily interested in the efficacy of land-use changes as a tool for mitigation. We found that the choice of land use is relevant concerning the average yearly carbon uptake and the emission reduction target of the European Union. However, carbon uptake remains small compared to fossil fuel emissions even under the land-use change scenario with maximum increase in forest area (Table 2).

Stakeholders from the agricultural sector were interested in soil organic matter content as a key factor in the carbon cycle and as an indicator of soil fertility. However, their greatest concern was the total amount of land available for farming. This may reflect that current agricultural subsidies disconnect farmers' success from actual ecosystem service supply, such as soil fertility and crop production. In some regions it is therefore questionable whether land that is "surplus" to food demands would readily be open for other uses.

The trends in European change drivers differ from global trends (*3*, *24*) in several ways:

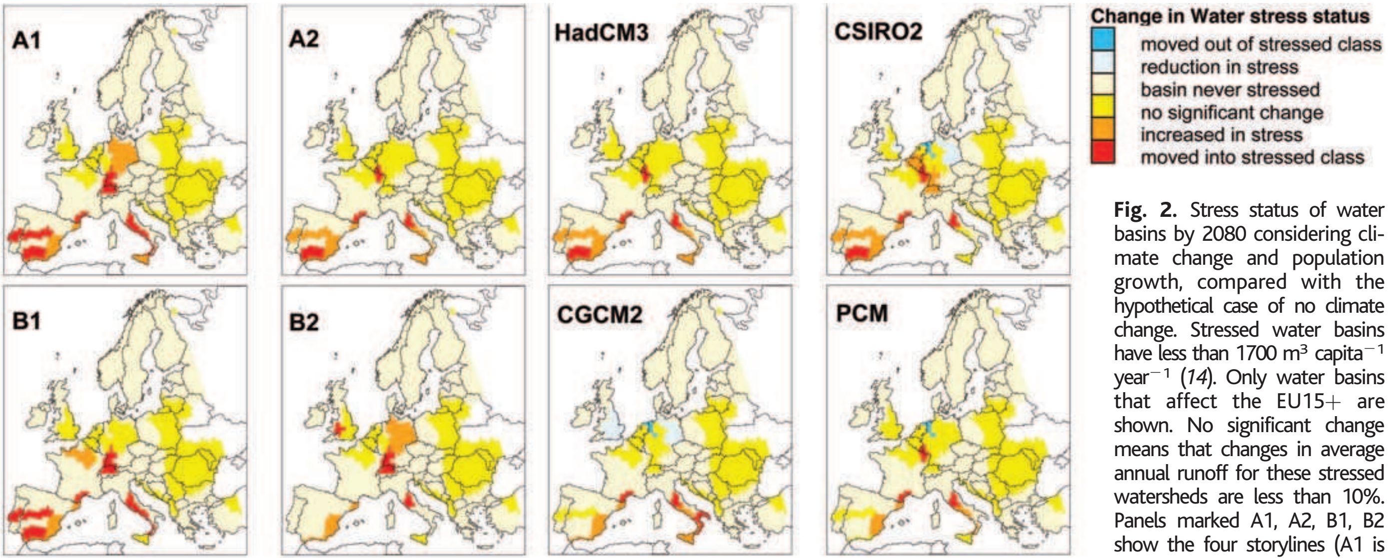

Fig. 2. Stress status of water basins by 2080 considering climate change and population growth, compared with the hypothetical case of no climate change. Stressed water basins have less than 1700 m^3 capita^{-1} year^{-1} (*14*). Only water basins that affect the EU15+ are shown. No significant change means that changes in average annual runoff for these stressed watersheds are less than 10%. Panels marked A1, A2, B1, B2 show the four storylines (A1 is A1FI) based on HadCM3 climate (2051 to 2080) and respective population sizes. Panels marked HadCM3, CSIRO2, CGCM2, and PCM show the four GCMs (2051 to 2080; PCM is NCAR-PCM) and A2 population size.

Population increases moderately if at all, the extent of urbanization is relatively small, forest area increases, and demand for agricultural land decreases. This allows changes in land management that could decrease vulnerability. Problematic trends in the EU15+ are mostly climate related.

The range of potential impacts in Europe covers socioeconomic options (storylines) and variation among GCMs. For most ecosystem services the A1FI scenario produced the biggest negative impacts, and the B scenarios seemed preferable. However, a division into either "economic" (A scenarios) or "equitable and environmental" (B scenarios) does not reflect all societal choices, given that sustainability does not forbid economic prosperity (*3*). The four storylines help explore but do not contain our optimal future pathway.

Among all European regions, the Mediterranean appeared most vulnerable to global change. Multiple potential impacts were projected, related primarily to increased temperatures and reduced precipitation. The impacts included water shortages, increased risk of forest fires, northward shifts in the distribution of typical tree species, and losses of agricultural potential. Mountain regions also seemed vulnerable because of a rise in the elevation of snow cover and altered river runoff regimes.

The sustained active participation of stakeholders indicated that global change is an issue of concern to them, albeit among many other concerns. The development of adaptation strategies, such as for reduced water use and long-term soil preservation, can build on our study but requires further understanding of the interplay between stakeholders and their environment in the context of local, national, and EU-wide constraints and regulations.

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4. Materials and methods are available as supporting material on *Science* Online.
5. The periods represent 30-year averages: baseline 1990 (mean over 1961 to 1990), 2020 (mean over 1991 to 2020), 2050 (mean over 2021 to 2050), and 2080 (mean over 2051 to 2080).
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Representation of Action-Specific Reward Values in the Striatum

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The estimation of the reward an action will yield is critical in decision-making. To elucidate the role of the basal ganglia in this process, we recorded striatal neurons of monkeys who chose between left and right handle turns, based on the estimated reward probabilities of the actions. During a delay period before the choices, the activity of more than one-third of striatal projection neurons was selective to the values of one of the two actions. Fewer neurons were tuned to relative values or action choice. These results suggest representation of action values in the striatum, which can guide action selection in the basal ganglia circuit.

Animals and humans flexibly choose actions in pursuit of their specific goals in the environment on a trial-and-error basis (*1*, *2*). Theories of reinforcement learning (*3*) describe reward-based decision-making and adaptive choice of actions by the following three steps: (i) The organism estimates the action value, defined as how much reward value (probability times volume) an action will yield. (ii) It selects an action by comparing the action values of multiple alternatives. (iii) It updates the action values by the errors of estimated action values. Reinforcement learning models of the basal ganglia have been put forward (*4*–*6*). The midbrain dopamine neurons encode errors of reward expectation (*7*–*9*) and motivation (*9*), and they regulate the plasticity of the corticostriatal synapses (*10*, *11*). Neuronal discharge rates in the cerebral cortex (*12*–*15*) and striatum (*16*–*18*) are modulated by rewards that are estimated by sensory cues and behavioral responses. These observations are consistent with action selection through the reinforcement learning rule (*3*) and with the notion of stimulus-response learning (*19*, *20*). However, two critical questions remain unanswered: Do the striatal neurons acquire action values in their activity through learning? How is the striatal neuron activity involved in reward-based action selection? Here we show by using a reward-based, free-choice paradigm that the striatal neurons learn to encode the action values through trial-and-error learning and

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