the long term, the structure of the ecosystem. In addition, such anthropogenic nitrogen inputs into the NPO could also enhance N_2O production due to an increase in remineralization in association with enhanced export production levels and potentially stimulate denitrification (*1*, *23*). If similar trends are confirmed across the other major ocean basins, it would constitute another example of a global-scale alteration of the Earth system.

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SUPPLEMENTARY MATERIALS

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Supplementary Text
Figs. S1 to S7
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COGNITIVE PSYCHOLOGY

Forgetting the presidents

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Two studies examined how U.S. presidents are forgotten. A total of 415 undergraduates in 1974, 1991, and 2009 recalled as many presidents as possible and attempted to place them in their correct ordinal positions. All showed roughly linear forgetting of the eight or nine presidents prior to the president holding office at the time, and recall of presidents without respect to ordinal position also showed a regular pattern of forgetting. Similar outcomes occurred with 497 adults (ages 18 to 69) tested in 2014. We fit forgetting functions to the data to predict when six relatively recent presidents will recede in memory to the level of most middle presidents (e.g., we predict that Truman will be forgotten to the same extent as McKinley by about 2040). These studies show that forgetting from collective memory can be studied empirically, as with forgetting in other forms of memory.

The name of the president of the United States is known to virtually all adult Americans. When doctors wish to test the cognitive status of a concussion or stroke patient, they often ask the patient to identify the current president; a response of "Ronald Reagan" in 2014, for example, reveals a probable deficit. Once they leave office, however, presidents recede from the memory of U.S. citizens. For instance, today presidents such as Fillmore, Pierce, and Arthur are barely remembered at all, yet at one point in America's past their names were known by all U.S. adults, just as the names Obama or Bush are known in 2014.

The purpose of this project was to study how presidents are forgotten from collective memory. Collective memory, sometimes called historical or popular memory, refers to the representation of the past shared by a group (*1*–*4*). Most studies in this tradition focus on how events of historical significance are remembered (e.g., the Holocaust, the 9/11 attacks), whereas our focus is on historical forgetting [see (*5*)].

We can assume that recall of a president is 100% while the president holds office and begins to drop when he leaves office. Our question is: What is the rate at which samples of U.S. citizens forget the presidents over time?

Across two studies, we determined the rate at which presidents recede from collective memory of (i) college students and (ii) a wider sample of Americans (taken from Amazon Mechanical Turk; MTurk). We measured memory for each president using both ordinal position recall and free recall criteria. Ordinal position recall describes whether an individual can place a president in the ordinal position in which he served (e.g., Lincoln in position 16). Free recall assesses whether an individual can recall a president's name at all, regardless of ordinal position. To measure forgetting, we applied two methods to the resulting sets of data. We examined the decline in recall within each group of subjects from the current president at the time of testing to the next most recent and so on (i.e., the recency effect in recall within groups of individuals). In the second method, we computed forgetting curves for six presidents across three generations of college students.

In our first study, we tested three generations of college undergraduates in three widely separated years: 159 subjects in 1974 (*6*), 106 in 1991 (*7*), and 150 in 2009. In each case the students were given a sheet of paper numbered according to the number of presidents (e.g., numbers 1 through 41 in 1991), with instructions to try to recall as many presidents as possible and to place them in their correct ordinal position. Students were told that if they recalled a president but not his ordinal position, they should guess or simply list that president off to the side of the page. They were given 5 min for recall, which prior research has shown is sufficient time to exhaust students' knowledge (*8*). Figure 1A shows recall of presidents as a function of their chronological term in office, when students were given credit for

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recalling them only if placed in their correct ordinal position; Fig. 2A shows free recall of the presidents, giving credit for naming the person without regard to order.

In laboratory studies in which subjects are given a list of words or pictures to remember, a serial position function is obtained relating list position to probability of recall. This function is characterized by two components of interest: (i) the primacy effect (enhanced recall of items at the beginning of the list), and (ii) the recency effect (enhanced recall of items at the end of the list), both relative to lower recall of items in the middle of the list. The recency effect is of interest for our purposes because it shows how items are forgotten over time. Namely, the last item in a series is almost perfectly recalled, with preceding items showing systematically lower recall as a function of the amount of time or the number of intervening items (presidents in our case), counting backward from the most recent. See fig. S1 for an example of a serial position function for word lists.

Another characteristic of the serial position function is that a distinctive event (relative to other events that are similar in character) is well remembered even if it is in the middle of a list. For example, a picture appearing in the middle of a list of words is recalled better than the surrounding words [the isolation effect (*9*–*11*)]. This feature occurs in our studies with a natural series rather than a list.

Figure 1A shows that memory for ordinal position of presidents follows a classic serial position function. All three groups showed a similar pattern of results: The first presidents were frequently recalled, with a steep drop until Lincoln, who showed elevated recall along with the two succeeding presidents (A. Johnson and Grant). This outcome is similar to the isolation effect in list recall, with Lincoln (or perhaps the U.S. Civil War) serving as the distinctive event. Recall then dropped back to a low baseline until the recency effect became noticeable. Even though the three groups of students were tested over a 35-year time period, the recency effect was remarkably consistent in that it occurred for the last 9 or 10 presidents in all groups. In addition, recall of presidents before the point of recency (located in what is called the pre-recency portion of the serial position curve) did not differ much among the groups; this point was confirmed in the second study (see below). The data also showed consistent forgetting of the order of recent presidents over time by different groups of college students. For example, in 1974 nearly all college students recalled L. Johnson and his ordinal position (*36*), but by 1991 the proportion had dropped to 0.52 and by 2009 it had plummeted to 0.20.

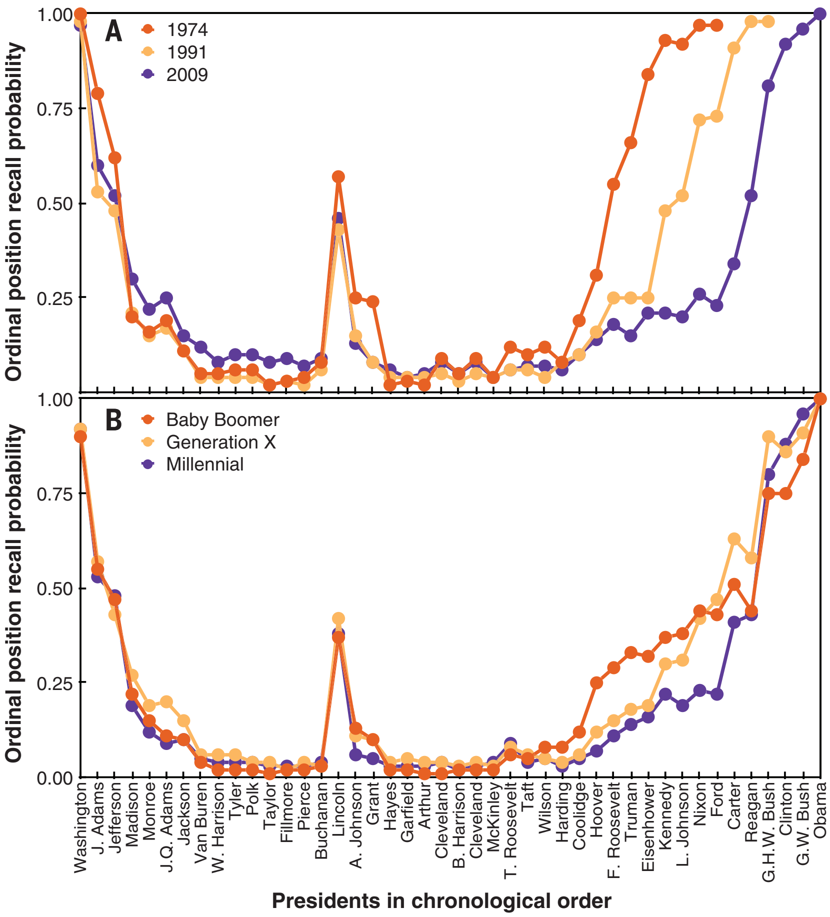

Fig. 1. Ordinal position recall probabilities. Ordinal position recall of presidents across (**A**) college students of three different generations (data collected in three different years) and (**B**) American adults of three different generations (data collected in 2014).

Whether presidents have been forgotten altogether, not merely with respect to their ordinal position, is better answered by plotting the data using a free recall criterion. These data, shown in Fig. 2A for the three groups of undergraduates, appear noisier than the data in Fig. 1A. Nonetheless, recency effects are still apparent, and what appears to be noise may rather reflect regularities in the memorability of presidents. For example, the dips at Truman, L. Johnson, and Ford occur in at least two samples and were confirmed in the second study.

A second method of measuring forgetting, the classic one in experimental psychology, is to plot the forgetting curve over time (or intervening items). The shape of this function—whether a logarithmic function or a power function—has been debated, but the power function provides a somewhat better fit when the two are directly compared (*12*). Moreover, these forgetting functions appear to be the same across many different tasks (*12*, *13*). Our data in Figs. 1A and 2A provide little evidence of forgetting for presidents prior to and including Coolidge. Memorability of these presidents seems to have reached an asymptote in U.S. students' collective memory. However, for presidents since Coolidge, we can fit a power function to the free recall data and estimate the rate at which they will be forgotten. We did this for the six most recent presidents for whom we had three data points (i.e., they had held office in 1974 or earlier): Truman, Eisenhower, Kennedy, L. Johnson, Nixon, and Ford. We assumed that these presidents had a 100% recall probability after leaving office and used the 1974, 1991, and 2009 data to estimate recall probability in those years. We fit power functions to the four points for each president. These forgetting functions are shown in Fig. 3, and it is apparent that Truman, L. Johnson, and Ford are fading fastest from historical memory in this group, whereas Kennedy has been better retained.

We can use these data to estimate the number of years that elapse before presidents fall to the baseline levels estimated by the line in Fig. 3 (the line represents a mean of 0.26, the average memorability of pre-recency presidents excluding Lincoln, his two successors, and the first seven presidents). Of course, with only four data points, the projections are tentative. They can be seen in Fig. 3, but to give one example, we estimate that Truman will be forgotten by three-quarters of college students (i.e., will reach 0.26 free recall probability) by 2040, 87 years after leaving office.

The data from the study described above were collected from students of the same age cohort (18 to 22) at three points in time across 35 years. In our second study, we used a complementary tactic: We tested adults across varying age ranges in May 2014 on the same task. We tested 116 adults aged 18 to 29 (millennials), 207 adults aged 30 to 49 (generation X), and 174 adults aged 50 to 69 (baby boomers) (*14*). These three generations correspond approximately to the three generations of college students that participated in the first study (e.g., college students in 1974 are the same group that we call baby boomers in 2014). We sought to determine whether the serial position curves obtained in our earlier studies would replicate with this larger sample of adults.

The data in Fig. 1B show that the answer is generally yes with strict positional recall, except that the recency part of the curve shows more overlap. In fact, recall of presidents from Washington to Coolidge reveals hardly any differences among the three age bands, and the data are similar to those in Fig. 1A. This lends support to our supposition from the first study that recall of these presidents has reached the asymptote of the forgetting curve. The differences emerge in the recency part of the curve, with older adults recalling more presidents in order than younger adults, at least from Coolidge through L. Johnson. Free recall results (Fig. 2B) again replicated the results in Fig. 2A reasonably well. The correlations between the patterns of data of people of similar age in Fig. 1, A and B, were r = 0.91, 0.95, and 0.98 for the baby boomer, generation X, and millennial samples, respectively (i.e., the data collected in 1974 correlated 0.91 with the data collected for the baby boomer group assessed in 2014). The similar values for the free recall data in Fig. 2, A and B, were r = 0.93, 0.94, and 0.97. All correlations were significant (P < 0.001); see tables S1 and S2 for the full correlation matrices. These strong correlations indicate that serial position curves in recall of U.S. presidents are remarkably similar and stable across age and across generations spanning 35 years.

The results from our two studies show forgetting of presidents in terms of their correct ordinal position in office (Fig. 1) and simply their name and the fact that they served (Fig. 2). The recency effect indicates that subjects can retrieve presidents relatively well if the presidents held office during or just before the subjects' lifetimes, but that recall of correct ordinal position drops as one attempts to retrieve presidents whose terms were more distant in time. By analogy to serial position curves in recall of lists, recent presidents appear to exist in a state of heightened accessibility, shown by the greater recency effect that is akin to a short-term component for other memory tasks involving recent events or people [according to one theory (*15*); see also (*16*)]. That is, collective memory has a window on the past that recedes, although doubtless through mechanisms different from those involved in short-term recall of lists.

Another interesting finding in our data is how consistently the pre-recency presidents are remembered across generations of students in the first study, as confirmed by the replication in our second study. All samples also recalled Lincoln and his immediate successors better than most presidents and also recalled their ordinal positions. Why are these data so consistent? A possible explanation is that presidents who are viewed as having been more historically influential are better remembered across generations. According to one theory (*17*), forgetting is adaptive and corresponds to environmental demands for needs of information. By this view, recall of presidents may be due to their frequency of mention in popular media, and frequency of mention may be determined by importance. To investigate, we correlated the recall scores from our second study with presidential rankings provided by history scholars and others (*18*). The correlation between recallability and ranking for presidents from Washington to Coolidge was high [$r(27)$ = 0.73, P < 0.001]. This finding is in line with the theory and data in (*17*).

Another theory argues that position in a series accounts for some of the variance in presidential

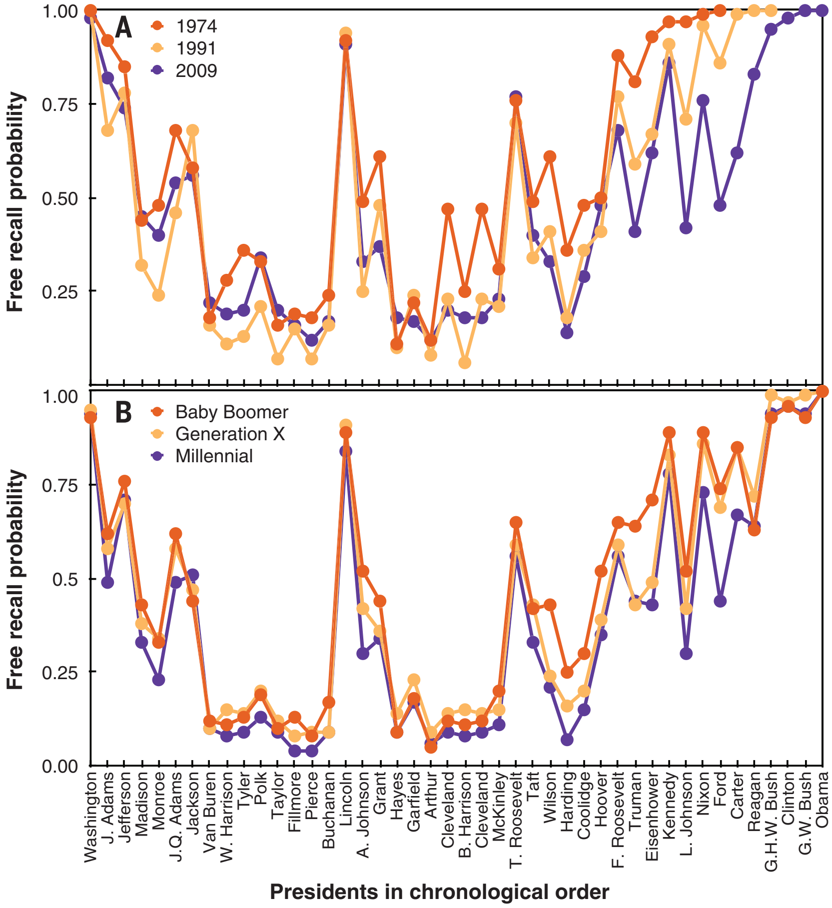

Fig. 2. Free recall probabilities. Free recall of presidents across (**A**) college students of three different generations (data collected in three different years) and (**B**) American adults of three different generations (data collected in 2014).

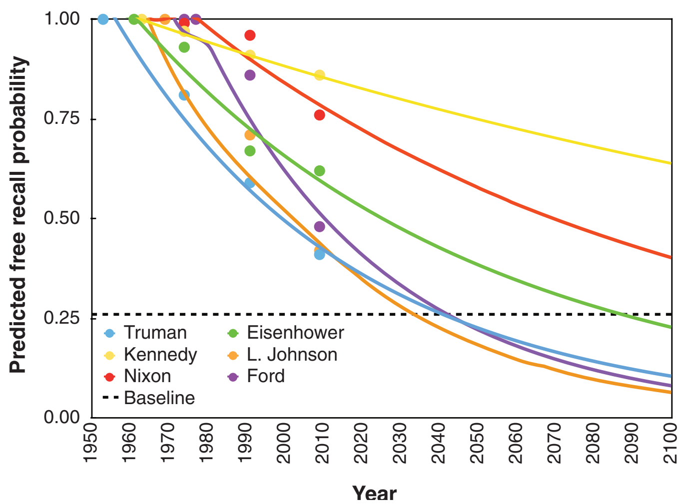

Fig. 3. Predicted forgetting curves. Forgetting curves for six presidents were predicted using the power function and data from the three generations of college students. The points show the original data.

recall (especially ordinal position recall), perhaps explaining why the second president, John Adams, is recalled in position better than Thomas Jefferson, a figure of greater historical importance (*6*, *7*). Other researchers have supported this claim (*19*, *20*), but there are also dissenters (*21–23*). Clearly Lincoln and his successors are well remembered because of their association with the American Civil War and the ending of slavery, but it is notable that many students and adults also often know that Lincoln was the 16th president. This superior recall of a salient event in a series resembles the isolation effect in list recall (*9–11*).

Our results show that memories of famous historical people and events can be studied objectively [see also (*4*, *5*, *24*, *25*)]. We find two different functions that characterize forgetting of the presidents. First, for individuals, memory for the order of presidents who served in office during the individual's lifetime (or a few years before) declines linearly. Second, forgetting of presidents across generations follows a power function until an asymptote is reached, in line with data from many other domains [(*12*, *13*); see (*5*) for similar results]. The asymptote probably reflects both the importance and frequency of mention of the particular president (*17*). The other notable feature of our results is the highly consistent recall of presidents by college students from several universities across a spread of 35 years, as well as by other Americans recruited from MTurk in 2014. The high correlations point to a great stability in how the presidents are remembered across generations—a seemingly permanent form of collective memory [i.e., semantic memory (*26*)].

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S3
Tables S1 and S2
References (*27–31*)
Data

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MITOCHONDRIA

Cell cycle–dependent regulation of mitochondrial preprotein translocase

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Mitochondria play central roles in cellular energy conversion, metabolism, and apoptosis. Mitochondria import more than 1000 different proteins from the cytosol. It is unknown if the mitochondrial protein import machinery is connected to the cell division cycle. We found that the cyclin-dependent kinase Cdk1 stimulated assembly of the main mitochondrial entry gate, the translocase of the outer membrane (TOM), in mitosis. The molecular mechanism involved phosphorylation of the cytosolic precursor of Tom6 by cyclin Clb3-activated Cdk1, leading to enhanced import of Tom6 into mitochondria. Tom6 phosphorylation promoted assembly of the protein import channel Tom40 and import of fusion proteins, thus stimulating the respiratory activity of mitochondria in mitosis. Tom6 phosphorylation provides a direct means for regulating mitochondrial biogenesis and activity in a cell cycle-specific manner.

Mitochondria are crucial for numerous tasks, from adenosine 5′-triphosphate synthesis and metabolism of amino acids, lipids, iron, and heme to apoptosis (*1–8*). Mitochondria cannot be formed de novo, but can be formed only by growth and division of preexisting organelles. Growth of mitochondria depends on the import of a large number of cytosolically synthesized precursor proteins. Multiple pathways of protein import into mitochondria have been identified (*2*, *3*, *9*). Nearly all pathways use the main mitochondrial entry gate, the translocase of the outer membrane (TOM). Mitochondria form a dynamic network that is continuously remodeled by fusion and fission events that, together with cytoskeleton-dependent transport and anchoring in daughter and mother cells, ensure a proper distribution of mitochondria during cell division (*5*, *7*, *10–13*). Cell cycle–dependent regulation of mitochondrial components has been observed in a few cases, including activation of the fission protein Drp1, of respiratory complex I, and of a mitochondrial DNA binding protein; the fusion protein Fzo1 is degraded upon arrest of yeast cells in G_1 phase (*14–19*). Whereas mitochondrial protein import is regulated by cytosolic kinases under different metabolic conditions (respiratory versus nonrespiratory) (*20*, *21*), whether protein import and the cell cycle are connected is not clear.

We used budding yeast as model organism to study the mitochondrial protein import machinery in different phases of the cell cycle.

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