

# Long-term studies provide unique insights into evolution

<https://doi.org/10.1038/s41586-025-08597-9>

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Received: 9 July 2024

Accepted: 6 January 2025

Published online: 19 March 2025

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From experimental evolution in the laboratory to sustained measurements of natural selection in the wild, long-term studies have revolutionized our understanding of evolution. By directly investigating evolutionary dynamics in real time, these approaches have provided unparalleled insights into the complex interplay between evolutionary process and pattern. These approaches can reveal oscillations, stochastic fluctuations and systematic trends that unfold over extended periods, expose critical time lags between environmental shifts and population responses, and illuminate how subtle effects may accumulate into significant evolutionary patterns. Long-term studies can also reveal otherwise cryptic trends that unfold over extended periods, and offer the potential for serendipity: observing rare events that spur new evolutionary hypotheses and research directions. Despite the challenges of conducting long-term research, exacerbated by modern funding landscapes favouring short-term projects, the contributions of long-term studies to evolutionary biology are indispensable. This is particularly true in our rapidly changing, human-dominated world, where such studies offer a crucial window into how environmental changes and altered species interactions shape evolutionary trajectories. In this Review article, we showcase the groundbreaking discoveries of long-term evolutionary studies, underscoring their crucial role in advancing our understanding of the complex nature of evolution across multiple systems and timescales.

Evolution can be predicted in the short term from a knowledge of selection and inheritance. However, in the long term evolution is unpredictable because environments, which determine the directions and magnitudes of selection coefficients, fluctuate unpredictably. (ref. 1)

Over the past century, evolutionary biology has entered—and embraced—its mechanistic epoch. From laboratory studies of microorganisms and multicellular model systems<sup>2–4</sup> to field studies of plants and animals<sup>5–7</sup>, evolutionary processes are being uncovered in unprecedented detail<sup>8</sup>. Long-term studies have proven particularly powerful, despite comprising only a small proportion of evolutionary biology research. Over the past several decades, a handful of pioneering long-term study systems have transformed our understanding of evolution through novel, sustained investigations. Peter and Rosemary Grant’s longitudinal field study of Darwin’s finches in the Galápagos—spanning 40 years and multiple species—has provided groundbreaking insights into temporal patterns of natural selection<sup>16</sup> and how speciation can unfold in the wild<sup>9</sup>; the Long-Term Evolution Experiment (LTEE) initiated by Richard Lenski, comprising 12 laboratory populations of *Escherichia coli* that have been evolving for more than 75,000 generations<sup>10</sup>, has uncovered general principles of evolutionary dynamics<sup>3,11,12</sup>; and the ongoing Park Grass Experiment, originally established in 1856, provided some of the first experimental evidence for rapid local adaptation over very small geographical distances<sup>13,14</sup>. However, such long-term evolutionary investigations

are exceptions. Most empirical studies measure evolutionary dynamics in the short term<sup>15,16</sup>, illuminating only a snapshot in time. Nearly three-quarters of evolutionary field studies measure natural selection across five or fewer time periods<sup>15</sup>—nearly one-quarter just once—and the vast majority of laboratory evolution studies operate on comparatively similar short timescales<sup>4,16</sup>. It is important to note that the relevance of these timescales depends on the generation time of the study organisms and the timescale over which selective events vary. Nevertheless, and although undoubtedly powerful, these approaches have limits in their ability to discern evolutionary patterns and mechanisms, which are inherently shaped by complex interactions operating at multiple temporal and spatial scales. Long-term evolution studies thus fulfil a critical scientific niche, often revealing processes that could be impossible to predict a priori or to examine experimentally<sup>17,18</sup>. They can identify oscillating, random or systematic changes over time, uncover time lags between environmental changes and population responses, and allow weak effects to accumulate into detectable patterns. Multiple short-term studies cannot substitute for this continuous, long-term perspective provided by extended research programmes. Even if able to capture rare events, short-term studies may be limited in their ability to interpret the evolutionary consequences of such phenomena<sup>6</sup>. Nevertheless, long-term studies are rare owing to their inherent difficulty, requiring an extraordinary level of dedication, focus and sustained research funding; occupying entire careers—or even those of multiple generations of scientists.

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## Types of long-term evolutionary studies

Scientists have relied on three key approaches to empirically examine long-term evolutionary processes through the continuous study of single systems. Although other subfields of evolutionary biology also investigate long-term patterns, such as those considering the fossil record, the focus of this article is on approaches that enable researchers to examine the mechanisms and dynamics of evolutionary change as they unfold in contemporary populations, offering unique insight that may be difficult or impossible to obtain otherwise.

### Observational field studies

From Darwin's finches in the Galápagos<sup>1,6</sup> to Soay sheep in the Outer Hebrides<sup>19,20</sup>, direct and unmanipulated long-term sampling of natural populations<sup>17,18</sup> has documented evolutionary changes in real time as they occur in nature, incorporating the complexities of natural environmental fluctuations, population demographics and species interactions. Moreover, observational field studies allow researchers to capture both rare and gradual processes that cannot be reliably examined in shorter studies.

### Experimental field experiments

Field experiments—scientific studies conducted in natural settings in which one or more factors are manipulated by the researcher—offer a powerful tool for investigating the causal links between environmental factors and evolutionary outcomes in natural settings. Field experiments can modify the environment in ways that observational studies, which are constrained by the inherent limitations of studying naturally occurring phenomena, cannot. In this way, study organisms can be exposed to conditions that otherwise may not be experienced. Critically, the ability to account for variation between experimental populations, such as differences in the environment or variation in genetic composition, as well as implementing experimental control treatments—groups or conditions in an experiment that receive no manipulation and serve as a baseline for comparison with the treated groups—allows for robust statistical inference, providing strong evidence for causal relationships that could otherwise remain difficult to identify. There are two basic approaches for long-term evolutionary field experiments: manipulative treatments maintained consistently throughout the experiment, such as in the British Park Grass Experiment<sup>13</sup> and the Illinois long-term selection experiment<sup>21</sup>, or establishing a long-term evolutionary perspective through a series of successive studies operating within a cohesive research framework. For example, long-term experimental studies of tropical guppies in Trinidadian streams<sup>22–24</sup> and *Anolis* lizards on small Bahamian islands<sup>25</sup>, both initiated in the 1970s and still ongoing, have investigated adaptive evolution and subsequent eco-evolutionary feedbacks over decades of abiotic and biotic selection pressures in natural settings<sup>22,25,26</sup>.

### Laboratory studies

From single-celled to multicellular microorganisms, microbial populations have provided remarkable insights into the dynamics of evolution across thousands of generations<sup>4</sup>. Although these studies are limited to organisms that can be maintained under laboratory conditions, they enable an exceptional level of environmental control and offer researchers unparalleled opportunities to examine the role of chance and historical contingency in evolutionary processes through the creation of initially identical replicate populations. One distinctive feature of many of these study systems is the ability to cryogenically store samples throughout the duration of the experiment that can be resurrected in the future, creating a living 'frozen fossil record'. These samples create a unique level of future-proofing—making the studies robust to future technological advancements—extending the usefulness of long-term laboratory studies by allowing historical populations to be retrospectively re-examined as novel analytical technologies are

developed. The potential loss of ecological realism in this approach is balanced by its experimental power: with the capacity to resurrect the entire evolutionary history of study populations under the precise environmental conditions they evolved in, a wide range of evolutionary hypotheses can be explored at will.

In the following sections, we review how these diverse methods for studying long-term evolutionary dynamics have advanced five critical areas of evolutionary biology.

## Bridging the process–pattern divide

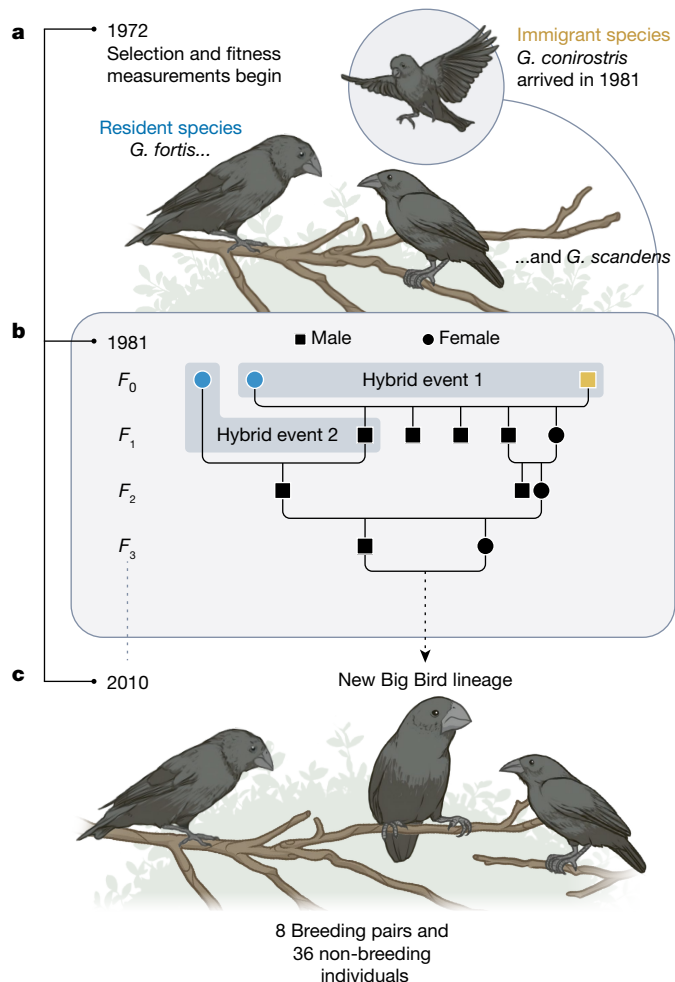
The study of evolutionary biology has traditionally been divided into two distinct domains<sup>27</sup>: microevolution, which focuses on the evolutionary processes occurring within a species, and macroevolution, which investigates patterns of evolution above the species level<sup>28</sup>. However, this conventional dichotomy has limited our ability to understand the interconnected relationship between evolutionary process and pattern<sup>28</sup>. For example, how do new species arise, and why do they often show a long period of stasis when contemporary populations typically possess the capacity for rapid evolution? How do novel innovations initially evolve, and how do they shape macroevolutionary trajectories? Long-term studies are the key to bridging this process–pattern divide: connecting short-term microevolutionary dynamics measured in real time to how long-term evolutionary patterns manifest over the duration of a study. In the following sections, we explore major questions that bridge this process–pattern divide and highlight the unique insights provided by long-term studies.

### How do multicellular organisms evolve from single cells?

The evolution of multicellularity is among the most important transitions in the history of life, yet the processes that lead to it remain unresolved as all known transitions occurred more than 250 million years ago<sup>29</sup>. The ongoing Multicellularity Long-Term Evolution Experiment<sup>2</sup> (MuLTEE) is examining the mechanisms and dynamics of this evolutionary transition in real time. Replicate populations of simple group-forming 'snowflake' yeast—a *Saccharomyces cerevisiae* mutant that grows as fractally branching multicellular clusters—are passaged with daily selection for larger multicellular size<sup>2</sup>. The physics of cellular packing gives rise to the first multicellular life cycles<sup>30,31</sup>, within which novel, highly heritable multicellular traits arise via both genetic and epigenetic mechanisms<sup>2,32,33</sup>. Snowflake yeast are initially small and brittle, but, over 3,000 generations, have evolved to become tens of thousands of times larger and as tough as wood<sup>2</sup>. The long-term value of the MuLTEE lies in its ability to prospectively explore how simple multicellular groups gradually evolve into increasingly integrated multicellular organisms, providing a window into evolutionary processes that cannot easily be reconstructed by looking backwards in time.

### How are new species formed?

The formation of new species is one of the most fundamental and important processes in evolution, yet one that has also proven spectacularly difficult to study directly<sup>34,35</sup>. One of the most compelling examples documenting the process of speciation comes from the Grants' longitudinal research of natural selection in a community of Darwin's finches on the small island of Daphne Major in the Galápagos. In 1981, 8 years into the study, a single male large cactus finch (*Geospiza conirostris*), a species not normally found on Daphne Major, immigrated from the island of Española over 100 km away<sup>9</sup> (Fig. 1). This bird successfully reproduced with two female medium ground finches (*Geospiza fortis*), producing offspring that gave rise to a genetically divergent lineage of birds. Subsequently named the 'Big Bird' lineage, these birds were strikingly different from either of their parental species, possessing larger body size, bigger beaks and a distinctive song<sup>6</sup>. Multi-generational pedigree analysis revealed that, by the third generation, members of



**Fig. 1 | Rapid hybrid speciation of Darwin's finches on Daphne Major island in the Galápagos<sup>6,9</sup>.** **a**, Nine years after the field study commenced in 1972, a single male large cactus finch (*G. conirostris*) emigrated over 100 km from Española island to Daphne Major. **b**, The cactus finch bred with a resident medium ground finch (*G. fortis*) female (hybrid event 1). A male produced from this initial hybrid event subsequently bred with a different *G. fortis* female (hybrid event 2). **c**, Within three generations, the hybrid lineage—named the Big Bird lineage owing to both larger body and bill sizes than either of the parental species—had become reproductively isolated through a combination of assortative mating via song and morphology. The rare event of island colonization by a single male *G. conirostris*, as well as the observations of how hybridization can produce reproductively isolated lineages, was possible due to the long-term and multifaceted sampling of this community. Figure was adapted with permission from ref. 9, AAAS. Credit: Mark Belan.

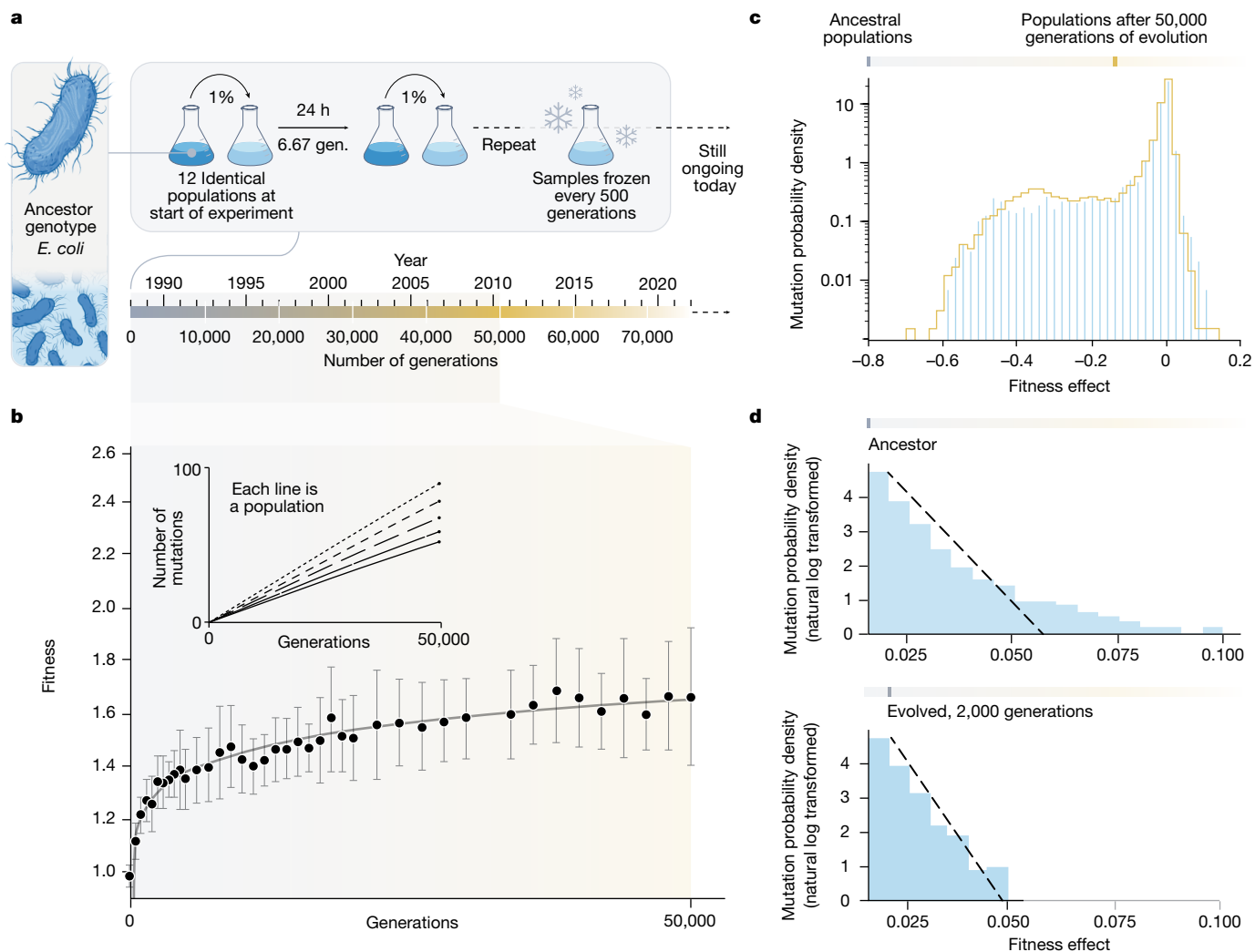
this new lineage were breeding exclusively with each other<sup>9</sup>. Through a combination of assortative mating by song type, niche divergence via shifts in beak size, and a drought that reduced the population size of a competitor species, the hybrid lineage had successfully established a breeding population and evolved reproductive isolation<sup>9</sup>: a hallmark of speciation<sup>34</sup>. Specifically, this case study highlighted how the combination of song preference and cultural inheritance of song type could be powerful facilitators of the evolution of reproductive isolation, and lead to speciation. Without multigenerational sampling and the serendipitous detection of the initial hybridization through careful and thorough observation, this outstanding case of hybrid speciation in the wild may have gone unnoticed. Crucially, the long-term nature of this research programme revealed the myriad interacting forces that led to the formation of this new species: a process far more complex than most theories of speciation often predict<sup>34</sup>.

## How do innovations evolve?

From powered flight in birds, bats and insects<sup>36</sup> to sticky toepads in arboreal lizards<sup>37</sup>, the role of novel phenotypes—innovations—has been widely acknowledged as a powerful trigger of evolutionary diversification<sup>36,38,39</sup>. Innovations, sometimes referred to as 'evolutionary'<sup>40</sup> or 'key'<sup>41</sup> innovations, generally refer to new traits that enable organisms to interact with the environment in a novel way. However, making a compelling case for cause-and-effect relationships between the emergence of an innovation and subsequent evolutionary dynamics is notoriously challenging<sup>38,42</sup>. Arguably the most complete investigation of an evolutionary innovation derives from the LTEE of *E. coli* (Fig. 2). Established in 1988, the LTEE investigates the evolutionary dynamics of 12 replicate populations of *E. coli* derived from the same ancestral genotype. After approximately 14 years and 31,500 generations, 1 of the 12 *E. coli* populations diverged from its ancestral reliance on glucose as their primary source of energy and carbon, evolving the novel ability to grow aerobically on citrate (the Cit<sup>+</sup> lineage)<sup>12</sup>, an ever-present yet ignored compound included in their growth media as a buffer. The resulting Cit<sup>+</sup> lineage was incredibly successful, gaining a substantial competitive benefit over Cit<sup>-</sup> lineages that lacked this ability<sup>12,43</sup>. The evolution of citrate utilization was a major innovation in the context of the LTEE; although many other bacteria can grow aerobically on citrate, it is rare in *E. coli*<sup>44</sup>. The value of the long-term experimental framework here is unquestionable: by reviving ancient populations from different time points in the LTEE before the evolution of citrate consumption, it was discovered that the ability to evolve this innovation was contingent on several previous genetic changes that occurred after approximately 20,000 generations. While these 'potentiating' mutations arose in multiple lineages, the unique combination required for the evolution of the Cit<sup>+</sup> phenotype was realized in only a single lineage during the LTEE<sup>12,43</sup>. The emergence of this key innovation then altered the ecosystem<sup>45</sup>; the evolution of aerobic growth on citrate led to a transition from an environment with a single limiting resource, glucose, to an environment with at least five resources that were either shared or partitioned between the newly formed Cit<sup>+</sup> and Cit<sup>-</sup> clades. The Cit<sup>+</sup> discovery demonstrates the value of long-term approaches to studying evolution, underscoring how long-term studies such as the LTEE provide enormous power to capture rare or unlikely events of evolutionary importance. Indeed, as the LTEE passes 44,000 generations since the initial emergence of the Cit<sup>+</sup> mutation, the phenotype has still yet to evolve in any of the other 11 populations in the experiment<sup>10</sup>.

## What explains the 'paradox of stasis'?

Although long-term studies have the unique ability to capture rare events, such as the evolution of innovative mutations, their temporal range can also provide the clearest opportunity to empirically resolve the apparent disconnect between microevolutionary processes and macroevolutionary patterns. For instance, a pervasive pattern in the fossil record is that most species or lineages exhibit little net phenotypic change over extended geological timescales<sup>46</sup>. It is unclear why this pattern is so widespread given that contemporary microevolutionary studies demonstrate that rapid evolutionary change is common<sup>47,48</sup>. Resolving this paradox of stasis is a major outstanding challenge in evolutionary biology<sup>49,50</sup>. Long-term stasis could arise from consistent stabilizing selection that maintains a population on a stable adaptive peak over time<sup>51</sup>. However, evolutionary field studies rarely find evidence for such persistent stabilizing selection—or stabilizing selection at all—operating on natural populations<sup>47,52</sup>. Instead, directional selection appears to be the predominant form of selection in the wild<sup>47</sup>. Given this apparent disconnect between process and pattern, one possible explanation is that temporal fluctuations in selection, including directional reversals<sup>53</sup>, could lead to long-term stability as populations vacillate around an adaptive peak<sup>50,54</sup> rather than stay perfectly atop. The shape of the adaptive landscape, and so the location of adaptive



**Fig. 2 | Temporal trends in fitness and mutations in the LTEE with *E. coli*<sup>70</sup>.** **a**, Established in 1988, the LTEE comprises 12 populations initially seeded with identical *E. coli* ancestral genotypes that have been allowed to evolve under stable environmental conditions. Sustained assessments of the evolutionary dynamics of these populations have been ongoing for over 75,000 generations<sup>10</sup>. The LTEE provides an unrivalled window into the dynamics of long-term evolution, highlighting the crucial roles of chance, historical contingency, and convergence. Moreover, its long duration makes the LTEE uniquely suited for reconciling evolutionary process and pattern. Gen., generations. **b**, Mean fitness of LTEE populations over time is best described by a power-law function, whereas the number of mutations continues to accumulate linearly (inset).

Error bars represent the standard deviation of fitness values across different non-mutator populations at each generation point. **c**, The distribution of fitness effect (DFE) of mutations in populations at the start of the LTEE and after 50,000 generations of evolution are strikingly similar; most mutations are deleterious (fitness effect < 0). **d**, The DFE of beneficial mutations (fitness effect > 0) in the ancestor has a long tail, which largely disappears over the first 2,000 generations of evolution. The DFE of mutations remains largely static at macrotemporal scales, despite extensive variation through time and across replicate populations in the realized fitness consequences of individual mutations. Panel **b** was adapted from ref. 3, Springer Nature. Panels **c** and **d** were adapted with permission from ref. 70, AAAS. Credit: Mark Belan.

peaks, may also be dynamic in response to local environmental conditions<sup>6,55</sup>. Long-term studies provide the empirical data necessary to test this hypothesis. In field studies of birds<sup>1,6</sup>, lizards<sup>52</sup> and plants<sup>56</sup> within-generation bouts of stabilizing selection were rarely detected; instead, sequential episodes of opposing directional selection, weak stabilizing selection or even periods of no selection combined to result in long-term stasis<sup>52,57</sup>. By measuring multiple successive bouts of selection through time<sup>1,6,52</sup>, such field studies offer a resolution to the paradox of stasis that shorter field studies would have been precluded from identifying.

### Hypothesis-generating machines

In addition to exploring well-established research questions, long-term studies often uncover unexpected findings that generate entirely new hypotheses and research directions. These unanticipated events can

lead to the generation of novel hypotheses that provide impactful insights to the process of evolution. One of the unique advantages of many long-term studies is that these hypotheses can be tested using data collected in the past, often using future methods and technologies that were not available when the research was initially started. For example, advances in DNA sequencing technology have allowed researchers to revisit frozen populations of bacteria<sup>43</sup> and animals<sup>58</sup> facilitating the generation of powerful new research directions. In this section, we highlight how the structure of long-term studies can lead to novel discoveries and first-of-their-kind datasets, creating opportunities to generate and test evolutionary hypotheses that might otherwise have been missed.

### Do populations adapt to their local environment?

The study of evolutionary biology was transformed in the early to mid-twentieth century with the development of the 'modern synthesis'<sup>59,60</sup>.

Integrating Darwin's theory of evolution by natural selection with the principles of Mendelian genetics<sup>61</sup>, evolutionary biologists raced to develop theoretical frameworks describing the genetics of adaptation<sup>62–64</sup>. Although laboratory studies subsequently excelled in empirically testing these ideas, a clear understanding of the spatial scale of local adaptation of populations outside of the laboratory was still lacking. In this context, local adaptation reflects a pattern by which native, or 'local', genotypes have higher fitness than foreign genotypes in their local habitat<sup>65</sup>. One of the first experimental case studies came from the long-running Park Grass Experiment in Rothamsted, UK, first started in 1856. The experiment investigated the effects of continuous fertilizer application on local plant biomass and diversity of neighbouring experimental plots<sup>13</sup>, and has provided a suite of ecological insights into the role that nutrients—particularly nitrogen—have in driving local plant species composition, richness and soil characteristics (for example, pH)<sup>66</sup>. During the course of this experiment, biologists had also noted that—despite very close proximity—populations of sweet vernal grass (*Anthoxanthum odoratum*) in neighbouring experimental plots that received different fertilizer treatments exhibited different traits, such as total size or flowering phenology<sup>67</sup>. In the 1970s, over a century after the experiment was established, evolutionary biologists discovered that these trait differences were heritable<sup>14</sup>. An elegant evolutionary experiment was then conducted to demonstrate the adaptive nature of these differences: researchers moved individual *A. odoratum* plants to neighbouring plots receiving different experimental treatments. When fitness was subsequently measured, the researchers identified strong selection against these transplanted genotypes, providing dramatic evidence for local adaptive evolution of resident plants<sup>14</sup>. This observation of strong local adaptation was particularly surprising owing to the small spatial scale at which it occurred—between neighbouring experimental treatment plots and so within pollen dispersal distances of *A. odoratum*—suggesting that local adaptation persisted despite the potential for gene flow to homogenize populations<sup>13,14,67</sup>. Since this serendipitous evolutionary discovery, the Park Grass Experiment—and other equally influential long-term field experiments of plants<sup>68,69</sup>—have provided the conceptual launchpad for a diverse range of evolutionary hypotheses investigating how, why and at what scale local adaptive evolution occurs<sup>65</sup>.

### What are the long-term dynamics of adaptation?

As most studies of contemporary evolution operate on moderate time-scales, key questions persist regarding the nature of adaptive processes over extended periods. For example, does adaptation continue indefinitely in a stable environment, or does it cease once a population reaches a local fitness optimum? How does the rate of molecular evolution relate to that of fitness increase? And can general principles of adaptation be applied to different organisms and different environments? Answering these questions is virtually impossible in natural populations, as one ideally needs long-term historical records spanning thousands of generations under constant environmental conditions and forms of selection. Although these criteria are rarely met in nature, experimental evolution studies in the laboratory can provide such conditions and so represent an ideal system with which to examine the long-term dynamics of adaptation. For example, as discussed above, the LTEE involves 12 initially identical populations of *E. coli* that have been allowed to adaptively evolve in a stable environment for tens of thousands of generations (Fig. 2a). Even after 50,000 generations and no environmental changes, fitness continued to increase<sup>3,70</sup>. Rather than plateauing, the change in fitness over this time frame was best described by a power law, meaning the rate of improvement progressively slowed but did not stop. Unlike fitness, however, the rate of molecular evolution has been remarkably consistent (Fig. 2b). These findings from the uniquely long dataset generated by the LTEE have led to the hypothesis that fitness optima may rarely be reached; instead, adaptation can continue for very long time periods, even in stable environments. The

rate of adaptation in the LTEE is thought to be determined, in part, by global diminishing returns epistasis<sup>71–73</sup>: as a population becomes more fit, the average magnitude of beneficial mutations within a given genetic background declines. Although strongly beneficial mutations are quickly exhausted (few exist after just the first 2,000 generations; Fig. 2c,d), adaptation continues because of the large supply of progressively less beneficial mutations. As diminishing returns epistasis has now been recorded in diverse microbial evolution and synthetic biology experiments<sup>72,74,75</sup>, it is possible that it is a widespread and general phenomenon. This pattern probably arises due to the modular structure of biological systems: initial mutations confer large fitness gains by altering key functional modules in a coarsely beneficial way, and subsequent mutations in the same modules have smaller effects as the system becomes increasingly fine-tuned<sup>72</sup>. The LTEE started out with genetically uniform populations and studies evolution generated from de novo variation; other long-term experiments have shown the importance of selection acting on standing, or pre-existing, genetic variation. Selection on such pre-existing variation allows populations to adapt more rapidly than waiting for new beneficial mutations to arise. For example, a 600-generation selection experiment in *Drosophila* found that adaptation occurred largely through incomplete selective sweeps and selection on standing variation, rather than hard sweeps involving new mutations as observed in the LTEE<sup>76</sup>. Long-term studies of wild vertebrate populations have also generated landmark insights into the role of additive genetic variation in adaptive evolution. An analysis of lifetime fitness and pedigree data from 19 long-term studies of bird and mammal populations showed high levels of mean additive genetic variation in individual relative fitness,  $V_A(\omega)$ , which indicated substantial potential for natural selection to increase mean fitness over short timescales<sup>77</sup>. For instance, the observed levels of individual relative fitness could enable rapid evolutionary recovery from sudden large declines in fitness, with over half of the studied populations predicted to be able to rebound within 10 generations following a 30% decline<sup>77</sup>. These findings underscore the importance of long-term individual-based studies of wild populations in advancing our understanding of the fundamental mechanisms driving adaptive evolution in nature<sup>17,18</sup>.

### Does selection always beget evolution?

Evolutionary theory predicts that strong directional selection on heritable traits should lead to an evolutionary response<sup>5</sup>. Consequently, many field and laboratory studies implicitly assume that the detection of selection in traits known, or expected to be heritable, will inevitably drive evolutionary change. It has been surprising, therefore, for several long-term field studies to have shown that this is not always the case<sup>6,78–83</sup>. For example, in a nearly two-decade study of collared flycatchers (*Ficedula albicollis*) that involved survival estimates from over 23,000 individuals, annual directional selection favouring fledglings with longer limbs was nearly constant; yet, the population never evolved longer limbs<sup>79</sup>. Similarly, persistent selection for larger body size was consistently observed over 40 years of field sampling of Galápagos common cactus finches (*G. scandens*), yet average body size actually declined over this period<sup>6</sup>. Another long-term study in red deer (*Cervus elaphus*) on the Isle of Rum, Scotland, found evidence for positive directional selection on calf birth weight<sup>84</sup> and antler size<sup>78,85</sup>, both heritable traits, owing to their association with increased lifetime breeding success. However, no evidence of phenotypic or genetic change was found in either trait over the study period. These long-term datasets are particularly insightful because consistent directional selection—even if fluctuating in strength—may be expected to accumulate over extended time periods and lead to gradual evolutionary change. Although many explanations for these paradoxical patterns have been proposed—the role of deteriorating environments<sup>82,86</sup>, unmeasured selection operating against the known selection<sup>87</sup> and genetic conflicts between traits under selection<sup>88,89</sup>—for example, when selection is not occurring on



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the measured heritable trait but rather is on an inheritable correlated trait<sup>88,90</sup>, or gene transfer via introgressive hybridization<sup>6</sup>—long-term studies were crucial for both identifying these unexpected patterns and for developing subsequent testable hypotheses to explain them. Longitudinal evolutionary studies have thus shown that the often-implicit assumption that evolution will proceed in correspondence with patterns of trait selection observed over the short term may often be incorrect, even when traits have high heritability. These findings suggest that evolutionary outcomes over extended periods can be influenced by a complex interplay between factors that may be missed by short-term measures of selection on phenotypic traits<sup>91</sup>. This possibility is troubling given that most evolutionary field studies are short: nearly one-quarter measure selection only once over a single time period<sup>15</sup>, probably owing to shortcomings in funding for longer-term studies.

### Evolution in a changing world

Evolution is constantly shaping life on Earth in response to environmental changes that range from natural fluctuations in climate to the novel challenges imposed by human activities. A wide array of evidence now demonstrates the evolutionary responses of populations to dynamic changes in their environments. Long-term studies have been crucial to placing such observations into a broader evolutionary context, for example, in identifying time lags between climatic events and evolutionary outcomes. As organisms are increasingly exposed to a suite of both acute and chronic human-caused stressors, two questions arise: whether species are evolving in response to human activities, and whether they are evolving fast enough to persist.

#### Fluctuating selection in dynamic environments

Changing environments can strongly affect the fitness of organisms by causing changes in both the form and the strength of selection<sup>92</sup>. In the Galápagos, cycles of El Niño southern oscillation events lead to extreme swings in precipitation that influence plant growth and seed availability on islands such as Daphne Major<sup>1,6</sup>. The ecosystem effects of these precipitation cycles can indirectly lead to changes in selection on seed-eating ground finches (*Geospiza* sp.). For example, when droughts follow typical rainfall, small seeds are rare and quickly depleted; directional selection favours finches with large body size and beaks that are strong enough to crack open the hard woody seeds that are more abundant<sup>6</sup>. However, when droughts follow extreme rainfall, selection switches direction: small birds with pointy beaks, those able to take advantage of a rain-driven abundance of small and soft seeds most effectively, are at a selective advantage. Long-term studies are required to both capture these oscillations in the direction of selection and understand their proximal causes. Environmental stochasticity can also have important evolutionary consequences by reducing long-term population growth rates and altering selection pressures on life history traits. Across two decades, increased variation in early-life conditions weakened the strength of viability selection in Isle of Rum red deer (*C. elaphus*) and lowered the heritability of fitness-related traits<sup>93</sup>, which then slowed the rate of long-term evolution. On the island of St Kilda, annual population crashes of Soay sheep (*Ovis aries*) over 50 years depend not only on the immediate environmental conditions but also on the age and sex composition of the population itself<sup>9</sup>. Specifically, markedly different evolutionary dynamics can manifest under similar weather conditions owing to variation in the demographic structure of the population<sup>19</sup>. These two long-term study systems highlight the complex interplay between short-term environmental variation, population dynamics and life history evolution, which could be overlooked in short-term observations<sup>94</sup>.

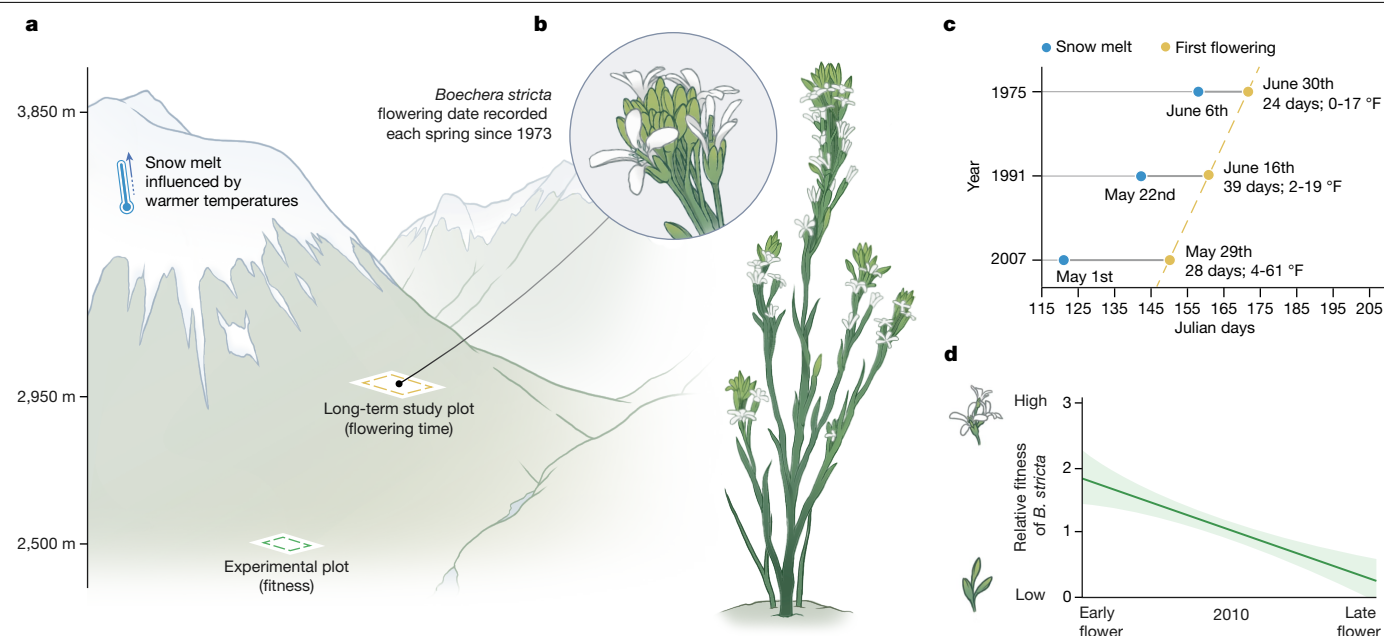
#### Climate and competition

The effects of climate cycles on resource availability can also accelerate the evolutionary effects of species interactions. Interspecific resource

competition, for example, can intensify if local climate conditions reduce resource availability, which can trigger divergent evolution through the process of character displacement<sup>95</sup>. Here again, the longitudinal study of Darwin's finches on the Galápagos has demonstrated its remarkable value to evolutionary biology<sup>6</sup>. Nine years into the study, the natural establishment of a small population of the previously non-resident large ground finch (*Geospiza magnirostris*) on the island of Daphne Major set the stage for competition with resident medium ground finches (*G. fortis*)<sup>96</sup>. Although character displacement did occur, it was not immediate, and was instead triggered by a period of intense drought 22 years later that limited seed availability. During this drought, *G. fortis* experienced strong directional selection for smaller beak sizes, which enabled the exploitation of smaller seeds and minimized competition with the larger-beaked *G. magnirostris*<sup>97</sup>. As beak size is highly heritable in these finches<sup>98</sup>, this single bout of selection was sufficient to drive an evolutionary shift resulting from this episode of character displacement over just one generation<sup>97</sup>. A decade later, newly developed genome sequencing techniques were applied to historic blood samples revealing a locus of major effect underlying this observation of character displacement<sup>99</sup>. By capturing the initial competitive encounter, the ecological context that triggered selection, the resulting evolutionary change in a key resource use trait and the genomic basis of that response, this long-term study provides a comprehensive view of the process of character displacement from start to finish that no short-term study could match.

#### Can species keep pace with climate change?

In addition to natural climate cycles, species must increasingly contend with the accelerated rate and magnitude of climate change driven by human activities. Long-term observational and experimental field studies have provided unique insights into the role of phenotypic plasticity and adaptive evolution in mediating organismal responses to anthropogenic climate change. One of the strongest observed signatures of climate change is phenological shifts in biological life cycles. In a series of long-term observational studies conducted since the 1970s at the Rocky Mountain Biological Laboratory in Colorado (Fig. 3), the flowering time of a perennial mustard plant, Drummond's rockcress (*Boechera stricta*), has shifted by approximately 3.7 days earlier per decade, tracking a trend of earlier snowmelt in the region<sup>100,101</sup>. Quantitative genetic analyses have demonstrated that this shift is due to phenotypic plasticity, with plants showing earlier flowering when exposed to earlier snowmelt dates<sup>102</sup>. Subsequent selection experiments have confirmed that this plasticity is adaptive, with earlier flowering genotypes experiencing higher fitness in years with early snowmelt<sup>100</sup>. In the UK, the advancement of great tit (*Parus major*) egg-laying by 14 days was also driven by adaptive plasticity<sup>103</sup>, which enabled the maintenance of phenological synchrony with a key food source (caterpillars) for offspring growth and development<sup>103</sup>. Similar patterns have been described from other long-term studies of organismal phenology. In Japan, mountain cherry trees (*Prunus jamasakura*) are currently flowering earlier than at any time since records began over 1,200 years ago<sup>104</sup>; in North America, a 143-year dataset of historical nest records has shown that egg-laying dates have advanced approximately 10 days across 72 species from 1872 to 2014 (ref. 105); and, in Sweden, an 18-year field study has identified advancements in the hatching phenology of blue-tailed damselflies (*Ischnura elegans*) across 16 populations. Subsequent analyses of over 1 million occurrence records of 49 other odonate species allowed the connection of the microevolutionary role that such phenological plasticity may have in driving adaptation to contemporary climate changes to broader macroevolutionary-scale range shifts that occurred in deep time<sup>106</sup>, further demonstrating the importance of long-term data to bridging the process–pattern divide in evolutionary biology. Shifts to earlier reproductive phenology also exist in mammals: on the Isle of Rum, parturition date of red deer (*C. elaphus*) has advanced by approximately 4.2 days per decade<sup>107</sup>. Quantitative



**Fig. 3 | Phenotypic plasticity and adaptive evolution contribute to advancing flowering phenology in response to climate change<sup>100,101</sup>.**

**a**, A series of long-term monitoring plots were established in 1973 at the Rocky Mountain Biological Laboratory (green dashed square) to monitor flowering phenology of Drummond's rockcress (*B. stricta*, Brassicaceae). **b**, Drummond's rockcress is a short-lived perennial mustard native to undisturbed habitats in the Rocky Mountains that produces white to pinkish flowers. **c**, From 1975 to 2016, the timing of first flowering in *B. stricta* advanced by 0.37 days per year, coinciding with a trend of earlier snowmelt in the region. Points represent the average Julian date of first flowering across seven 2 × 2 m plots and the average Julian date of snowmelt. **d**, Quantitative genetic field experiments in 2010

using recombinant inbred lines revealed strong directional selection favouring earlier flowering in *B. stricta*. Relative fitness, measured as fruit production, was highest for plants that flowered earlier than those that flowered later. The 38-year longitudinal dataset was crucial for detecting the advancing flowering time of *B. stricta* in response to climate change by capturing important inter-annual variation in response to snowmelt dates. These long-term data allowed researchers to disentangle the contributions of phenotypic plasticity and adaptive evolution to the observed phenological shift, highlighting the importance of maintaining long-term ecological monitoring programmes to understand evolutionary responses to climate change. Figure was produced using data from ref. 100, The Royal Society. Credit: Mark Belan.

genetic analyses have shown that this temporal trend is probably driven by a combination of both genetic change and phenotypic plasticity in response to warming temperatures<sup>107</sup>. Although these studies have demonstrated the potential for phenotypic plasticity to facilitate rapid adjustments to novel climatic conditions, they also highlight its limitations<sup>108</sup>. Current rates of plastic change either already lag, or are predicted to be increasingly asynchronous with, the rate of environmental change<sup>109</sup>. Moreover, there are limits to the range of conditions that can be accommodated by plasticity; in many cases, adaptive evolution will be necessary for long-term population persistence<sup>108</sup>. Nevertheless, plasticity could stabilize populations in the short term, buying time until adaptation can proceed from either standing genetic variation, de novo mutations or from novel alleles introduced by migrants from trailing edge populations<sup>110,111</sup>. It is imperative for evolutionary studies to continue disentangling the relative contributions of plasticity and genetic change in this context to better understand the long-term viability of wild populations in changing environmental conditions.

### Human activities as a driver of evolutionary change

Long-term studies have also shed light on the direct effects that human activities have had on evolutionary processes. Perhaps the most famous is the collection of studies carried out on the rise of the melanistic form of the peppered moth (*Biston betularia*) during the nineteenth and twentieth centuries in Great Britain<sup>112–114</sup>. Rapidly expanding industrialization produced air pollution that darkened the tree trunks on which these moths resided, which made the previously abundant white form of the moth increasingly conspicuous to bird predators. The resulting directional selection against the now phenotypically mismatched white form led to a rise in abundance of the melanistic form in industrialized areas<sup>112–114</sup>. Within a century, the melanistic form comprised over 90%

of all peppered moths in industrial areas<sup>115</sup>; further monitoring has revealed that, by 2010 and in concert with a post-industrialization reduction in air pollution, the frequency of the white form has resurged as the melanistic form becomes increasingly rare<sup>116</sup>, suggesting a reversal in the direction of selection. The evolutionary consequences of other types of human activity—both direct, such as harvesting, and indirect, such as ecosystem modification—will require similarly long-term investigations. For instance, analysis of a detailed 40-year dataset from Finland showed that the effects of direct harvesting of large breeding adults combined with the indirect effect of resource depletion of prey species has led to the rapid evolution of earlier maturation in Atlantic salmon (*Salmo salar*)<sup>117,118</sup>. Similar studies are needed for understanding how species are evolving in response to urbanization<sup>119,120</sup>, and whether insights from evolutionary biology can be used to develop strategies for the management of urban biodiversity<sup>120,121</sup>.

### Predicting evolution

Throughout the history of evolutionary biology, a long-standing and central debate concerns the degree to which evolution is predictable<sup>7,122–124</sup>. The debate centres on the relative contributions of random and deterministic processes to evolutionary outcomes<sup>122,125,126</sup>. Specifically, two main hypotheses have been proposed to explain difficulties that arise in predicting evolution<sup>127</sup>. The random limits hypothesis posits that prediction is limited by the fact that core processes—such as mutation, clonal interference or genetic drift—are inherently stochastic<sup>60</sup>, whereas the data limits hypothesis argues that even deterministic evolution driven by natural selection will be difficult to predict owing to insufficient information about selection pressures, environmental factors, trait variation and inheritance<sup>128,129</sup>. Below we discuss how

long-term laboratory studies of experimental evolution have been key to testing the random limits hypothesis, whereas long-term evolutionary field studies are ideally suited to assessing the extent to which our predictive ability is constrained by data availability.

## Convergence and contingency in evolution

Laboratory evolution experiments using initially identical replicate populations in the same environment provide an unparalleled opportunity to examine the repeatability of evolutionary processes and the extent to which randomness constrains evolutionary prediction<sup>122</sup>. In the LTEE, the fitness trajectories of nonmutators in the 12 replicate populations (shown in Fig. 2b) have been highly parallel: 51.1% of the variation in fitness over the first 50,000 generations was explained by the number of elapsed generations, whereas replicate population identity only explained 7.1% of the total variance in fitness (sum of both the main effect and interaction between population and time; two-way analysis of variance on log-transformed data,  $F_{23,898} = 81.7$ ,  $P < 0.0001$ ; data analysed from ref. 3). This demonstrates that the rate of adaptation in a constant environment can be predictable, which is consistent with the role of diminishing-returns epistasis in adaptation. Under this model, the fitness effects of new mutations are not random but depend on the fitness of the lineage in which they arise<sup>72,130</sup>. Indeed, fitness has evolved convergently in other microbial evolution experiments<sup>72,131</sup>, suggesting that this is a general phenomenon. Certain genetic changes, often those that are related to the selection pressure being imposed on the system (for example, metabolic efficiency<sup>132,133</sup> or antibiotic resistance<sup>134</sup>), are highly convergent and thus predictable. In the LTEE, about half of the non-synonymous mutations in the lines that retained the ancestral mutation rate occurred in just 57 genes. However, the overall spectrum of mutations was more variable. A total of 229 genes (approximately 80% of all genes gaining a mutation) were evolutionary singularities in which a single non-synonymous mutation occurred over 50,000 generations<sup>135</sup>. Parallelism at the level of specific mutations is considerably rarer<sup>135</sup>. The evolution of major innovations, such as aerobic growth on citrate, is especially difficult to predict, as it evolved in only one population after approximately 31,500 generations and was contingent on a particular history of ecological change and mutation accumulation, as described above<sup>43,136</sup>. The LTEE thus illustrates the constraints emphasized by the random limits hypothesis: even with identical starting genotypes and environments, the stochastic nature of mutations and long-term importance of historical contingency can lead to profoundly different evolutionary outcomes, fundamentally limiting the capacity for evolutionary prediction.

## Forecasting evolution in the wild

The data limits hypothesis, which posits that insufficient information about various ecological and evolutionary factors hinders our ability to predict evolution, has been recently tested using long-term evolutionary field studies. The historical sampling data available from such studies are vital for training predictive statistical models, whereas continued sampling permits testing of the predictive accuracy of the model. For example, Bayesian autoregressive moving average (ARMA) models have been used to assess the predictability of micro-evolutionary changes in the cryptic body coloration and pattern of wild Californian stick insects (*Timema cristinae*)<sup>137</sup>. Leveraging 25 years of field data, experiments and genomics, ARMA forecasting models have revealed that long-term changes in colour-morph frequencies are only modestly predictable (median predictive  $r^2 = 0.14$ ). These changes are governed by complex and fluctuating selective regimes; opposite directional selection occurs on melanistic forms during hot years owing to the positive effects of increased crypsis from predators on dry plants, but the negative effects of lower thermal tolerance of hot temperatures. However, changes in pattern-morph frequencies are highly predictable, as negative frequency-dependent selection in which more common morphs experience higher predation drives

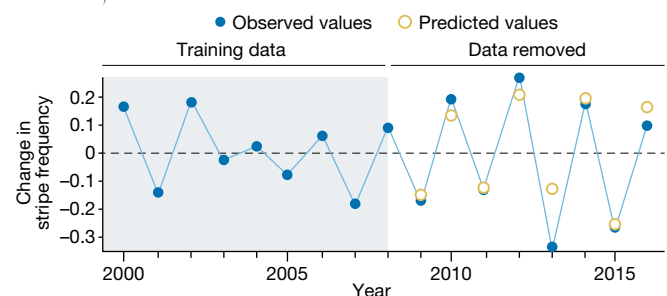
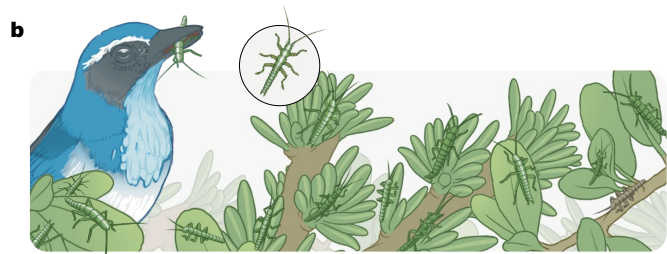
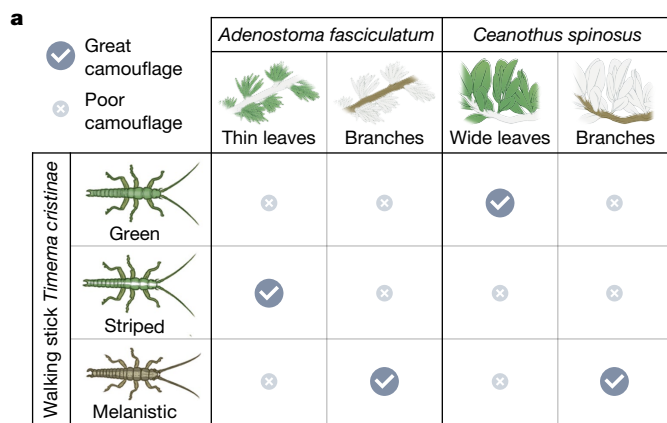
regular periodic fluctuations in morph frequencies ( $r^2 = 0.86$ )<sup>137</sup> (Fig. 4). When applied to ten independent datasets of *Timema* survival spanning in length from 10 to 30 years each, these patterns of negative frequency-dependent natural selection remain highly predictable<sup>138</sup>. The combination of extensive temporal sampling data from wild populations with short-term experiments of physiology and genomics was critical for quantifying the predictability of evolution and identifying the factors that influence it. The application of these statistical forecasting models to other long-term evolutionary datasets—including Darwin's finches (*Geospiza* sp.), scarlet tiger moths (*Panaxia dominula*) and peppered moths (*B. betularia*)—has been less successful (median predictive  $r^2 = 0.03$ – $0.18$ )<sup>137</sup>, demonstrating the predictive difficulty even in well-studied groups with long time series of historical data. To accurately forecast future patterns, detailed knowledge of the relationships between genotype and phenotype with fitness, trait heritability, the stochasticity of mutational processes, the potential for unexpected environmental perturbations, and how selection changes across space and through time is required. As capturing this complexity is inherently difficult<sup>129</sup>, current predictive models are limited in their ability to forecast evolutionary change.

Predicting evolution is complicated<sup>138–140</sup>. This is exacerbated by inconsistencies in what ‘prediction’ means, and how it is applied, in evolution<sup>141</sup>. The approaches previously discussed in relation to *Timema* stick insects offer only a limited view of predictability: how repeatable are population responses to known environmental conditions. A true predictive theory of evolution would involve forecasting what happens when populations are exposed to new conditions. For such a theory to exist, two advances are required: a clearer mechanistic understanding of how natural selection operates in the wild, and a more complete understanding of environments and trait performance<sup>142</sup>.

## Ecological consequences of evolutionary dynamics

Evolutionary biologists have traditionally focused on the unidirectional influence of ecological processes on evolutionary dynamics. More recently, the reverse relationship—how rapid evolution can drive ecological dynamics—is receiving increasing research attention<sup>143–145</sup>. Although the reciprocity of eco-evolutionary dynamics has been long recognized<sup>143–147</sup>, current advances focus on better understanding the entire feedback loop: how ecological factors drive local microevolutionary processes, leading to the emergence of novel phenotypes that can modify ecosystem dynamics, which in turn can subsequently reshape the selective pressures acting on these species, and so on<sup>144,148</sup>. However, although laboratory and mesocosm experiments have demonstrated convincing evidence for this eco-evolutionary feedback loop<sup>149–153</sup>, far less is understood about how these reciprocal dynamics manifest in more complex natural systems<sup>154</sup>. Long-running series of field experiments of freshwater guppies (*Poecilia reticulata*) in Trinidadian streams<sup>22</sup> and *Anolis* lizards (anoles) on Bahamian islands<sup>25,155</sup> have provided some insights to the complex interplay between eco-evolutionary dynamics over long timespans. In both guppies<sup>22,26,156–158</sup> and anoles<sup>159,160</sup>, the experimental manipulation of the presence of their primary predators rapidly changes the adaptive landscape. In guppies, this occurred via their translocation to freshwater pools free of predatory pike cichlids (*Crenicichla* sp.); in anoles, curly-tailed lizards (*Leiocephalus carinatus*) were introduced to the small islands supporting anole populations (Fig. 5). In both cases, there were short-term effects of adaptive change on the ecological dynamics of the system (that is, the evolution-to-ecology relationship): when guppies adapted to high-predation environments are introduced to pools without predatory pike cichlids, guppies reduce the abundance of freshwater invertebrates<sup>161</sup>; similarly, when ground-dwelling predatory lizards are introduced to predator-free islands, anoles experience strong directional selection, decreases in population size and increase in arboreality<sup>159,160</sup>. Consequently, with fewer anoles on the ground, population sizes of terrestrial arthropods increase<sup>25,162</sup>, and





plant herbivory by insects increases due to overall smaller anole population sizes<sup>163</sup> (Fig. 5). However, these short-term responses are different than the expected long-term patterns. In naturally predator-free pools, guppies limit the growth of freshwater algae and not invertebrates. Likewise, on predator-introduction anole islands, the short-term effects of increased plant herbivory disappear when the experiment is allowed to continue for multiple generations<sup>25</sup>. Although both study systems have enabled the development of a comprehensive understanding of how ecological conditions can drive evolutionary trajectories, the reverse relationship appears to remain difficult to predict. Sustained longitudinal sampling remains the clearest way to investigate these

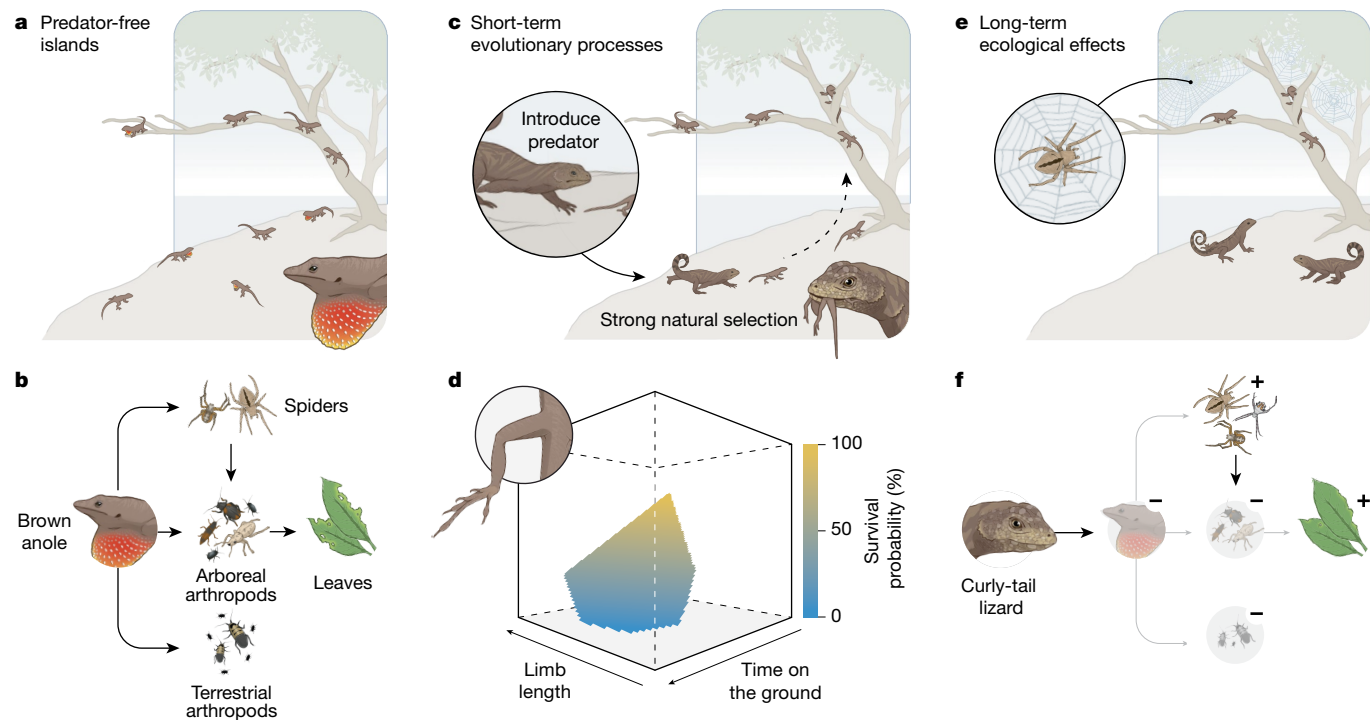
**Fig. 4 | Predicting evolution in response to natural selection<sup>137</sup>.** **a**, Californian stick insects (*T. cristinae*) exhibit three morphs that vary in colour, pattern and associated camouflage on their host plants. An unstriped green morph has high camouflage on the broad leaves of greenbark plants (*Ceanothus spinosus*), whereas the striped green morph is cryptic on the thin leaves of chamise plants (*Adenostoma fasciculatum*). The melanistic morph, which is brownish-grey and lacks stripes, is well camouflaged on the brown stems of both host plants but stands out on the leaves. **b**, Predation of *T. cristinae*, such as by the Californian scrub jay (*Aphelocoma californica*), is highest in the most abundant morphs each year. Higher survival in rare pattern morphs driven by negative frequency-dependent selection leads to highly predictable evolution of pattern morph frequency through time. **c**, In hot years, when leaves turn brown due to desiccation, melanistic morphs have a survival advantage from predation due to increased camouflage. However, melanistic morphs also have lower heat tolerance than green morphs, resulting in lower relative survival due to thermal physiological stress. The modest predictability of colour morph frequency is a result of the complex interaction between biotic (predation) and abiotic (climate) selection pressures. The application of Bayesian ARMA models, a statistical technique that uses time series data to predict future values based on past observations, was possible because of the long-term sampling of *T. cristinae* morphs over 25 years. By using a portion of the data to train the models and then validating the model predictions against the remaining long-term monitoring data, this study demonstrates the importance of longitudinal data in understanding and predicting the complex dynamics of evolution in natural populations. Figure was produced with data using ref. 137, AAAS. Credit: Mark Belan.

reciprocal dynamics and better investigate the role that microevolutionary dynamics have in ecosystem processes. Evidence for ecological feedbacks from evolutionary processes on short temporal scales is rapidly increasing<sup>143,144,150,164</sup>. However, as highlighted by these long-term studies of small Bahamian islands<sup>25</sup> and Trinidadian freshwater streams<sup>22</sup>, sustained investigations of such eco-evolutionary dynamics often reveal that immediate feedbacks may be ephemeral or weakly preserved through time. It is possible, therefore, that many ecosystems could be largely robust to small-scale evolutionary dynamics over long timescales. The only way to discern this possibility will be through sustained research providing the evidence needed to observe long-term effects.

## Perspective

Long-term processes require long-term study. (ref. 6)

Long-term studies have had a profound effect on our understanding of evolutionary processes, capturing dynamics that are obscured in short-term studies owing to the stochastic nature of evolutionary change and the time lag between cause and effect. However, despite their longstanding impact on the field, long-term evolutionary studies remain rare. The reason for this is multifaceted: long-term research programmes require an exceptional level of professional dedication and effort, may have unclear publication directions, and, most notably, are a poor fit for modern systems of research funding in which short-term (3–5 year) financial support predominates. To advance current long-term studies, as well as stimulate the inception of new studies, funding agencies therefore have a key part to play. Renewal of research funding often requires exciting new research questions and directions to be proposed: although this can happen in long-term studies, it is not guaranteed, and the core value of such research programmes lies in maintaining systematic collection of consistent data types through time. Funding bodies should consider dedicated support mechanisms for long-term evolutionary research, as already exists for ecological and environmental sciences<sup>165</sup>. This necessitates developing criteria to evaluate which studies are worth continuing by focusing on their potential to provide unique evolutionary insights that



**Fig. 5 | Investigating the evolution-to-ecology feedback cycle in island lizard communities<sup>25</sup>.** **a,b**, In the Bahamas, brown anole lizards (*A. sagrei*) on small islands live in high-density populations and occupy a wide variety of microhabitats (**a**); long-term ecological studies have documented the food web structure of these island ecosystems (**b**)<sup>25,155</sup>. **c,d**, When a large ground-dwelling predatory lizard, the curly-tailed lizard (*L. carinatus*), is experimentally introduced to the island, the brown anole population rapidly decreases in size and experiences a strong shift in natural selection (**c**). Specifically, the survival rate is lower for anoles that spend more time on the ground and are subject to

higher direct risk of predation (**d**)<sup>159</sup>. Directional selection also favours anoles with longer limbs<sup>159,160</sup>, which confer faster sprint speeds across the ground and facilitates escape from predator encounters. **e,f**, In response to the predator, brown anoles become more arboreal and the population significantly decreases in size, which changes the resource-flow dynamics of the entire ecosystem (**e**): brown anoles consume fewer terrestrial arthropods, spider density increases due to relaxed top-down effects of brown anoles, and plant leaves exhibit lower herbivory (**f**)<sup>25,162,163</sup>. Panel **d** was produced using data from ref. 159, AAAS. Credit: Mark Belan.

cannot be otherwise obtained. Similarly, many—if not, most—long-term research programmes are not initiated as such and evolve naturally out of short-term objectives. Insightful researchers, particularly those in the early stages of their career, able to identify the value in this transition are the reason for their success. Evolutionary biology will continue to prosper from early-career researchers initiating long-term studies.

### Looking to the future

The next century of long-term studies promises to reveal even more exciting developments in evolutionary biology. First, the integration of rapidly improving technology will continue to provide novel tools for investigating evolutionary dynamics. In the laboratory, genome-editing methods, such as CRISPR–Cas9 approaches<sup>166</sup>, are already available to provide direct functional tests of genes under selection in long-term evolutionary studies. In the field, advances in sensor technology promises to both accelerate and expand how evolution can be studied. From detailed quantification of the environment using remote-sensing technologies such as aerial LiDAR<sup>167</sup> to animal-borne sensors<sup>168,169</sup>, the integration of technological hardware will revolutionize evolutionary field studies by providing unparalleled insights into biotic and abiotic drivers of natural selection in the wild.

Second, the advent of machine learning and artificial intelligence offers powerful new approaches for analysing the complex, multi-dimensional datasets generated by long-term studies. Just as the innovative statistical framework of Lande and Arnold in the 1980s<sup>170</sup> stimulated decades of evolutionary field studies of natural and sexual selection<sup>171</sup>, future advances in analytical techniques—in partnership with greater computing power—could uncover subtle patterns and relationships that might be overlooked by traditional statistical methods.

Such advancements have the potential to reveal hidden evolutionary dynamics and shed light on previously unrecognized selective pressures acting on populations<sup>172</sup>. Moreover, applying these techniques to long-term genomic and phenotypic data could enable researchers to predict evolutionary trajectories with greater precision and accuracy. Machine learning approaches could also prove transformational for extracting information from both archived and newly collected data sources<sup>173</sup>, such as biological attributes in images, videos, acoustic and other data-rich sources<sup>174</sup>.

Third, the integration of evolutionary theory in epidemiology<sup>175</sup>—a major applied goal of evolutionary biology—will be increasingly nuanced by the accumulation of long-term datasets examining the evolution of medically significant pathogens, such as HIV<sup>176</sup> or COVID-19 (ref. 177).

Fourth, long-term datasets are invaluable to biological conservation: long-term studies provide a unique and ecologically realistic window into how species are evolving in response to global change, and if such shifts are keeping pace with these rates of environmental change<sup>108</sup>. These insights will be critical for developing conservation management strategies that account for ongoing evolutionary processes in threatened species and ecosystems.

Last, a particularly exciting—and tangible—advance will be in studies that synthesize the traditionally discrete research approaches discussed in this essay into single long-term evolutionary studies. For example, the hallmark of long-term field studies is the continuous longitudinal sampling of populations in the wild, whereas laboratory studies have exceptional control of the genotypic and phenotypic constitution of their study populations. A recent unification of these approaches was applied to continuous measurements of selection in

replicated isogenic populations of *Drosophila* in outdoor mesocosms exposed to natural environmental conditions<sup>178,179</sup>. Such studies have only operated at moderate timescales so far (10–12 generations), but— if extended—represent an expanding frontier in how evolutionary processes are studied in ecologically relevant contexts.

Conducting long-term research is challenging. Nevertheless, such research programmes are exceptionally valuable. These studies provide a powerful and unparalleled unified framework to examine both the processes and the patterns of evolution, unlocking insights into the fundamental evolutionary mechanisms that shape life on Earth. As such, they have a crucial role in advancing our understanding of evolutionary biology and will continue to be instrumental in shaping the future of the field.

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**Acknowledgements** We thank J. Anderson, Z. Blount, S. Brown, T. Grainger, J. Losos, M. Moore and K. Thompson for valuable feedback on earlier versions of this manuscript; B. Sheldon, D. Schluter and an anonymous reviewer for critical feedback that greatly improved our manuscript; and M. Belan (ArtSci Studios) for the illustrations. This work was supported by grants from the US National Institutes of Health (grant no. 5R35GM138030) and the NSF Division of Environmental Biology (grant no. DEB-1845363) to W.C.R.

**Author contributions** J.T.S. conceptualized the manuscript. J.T.S. and W.C.R. wrote the manuscript.

**Competing interests** The authors declare no competing interests.

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**Peer review information** *Nature* thanks Ben Sheldon, Dolph Schluter and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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