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The value of long-term ecological research for evolutionary insights

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Scientists must have an integrative understanding of ecology and evolution across spatial and temporal scales to predict how species will respond to global change. Although comprehensively investigating these processes in nature is challenging, the infrastructure and data from long-term ecological research networks can support cross-disciplinary investigations. We propose using these networks to advance our understanding of fundamental evolutionary processes and responses to global change. For ecologists, we outline how long-term ecological experiments can be expanded for evolutionary inquiry, and for evolutionary biologists, we illustrate how observed long-term ecological patterns may motivate new evolutionary questions. We advocate for collaborative, multi-site investigations and discuss barriers to conducting evolutionary work at network sites. Ultimately, these networks offer valuable information and opportunities to improve predictions of species' responses to global change.

Predicting species' responses to environmental change is increasingly important as global change continues to alter ecosystems worldwide[1–3]. Global change may require species to evolve at a pace that matches environmental change to persist[4]. Fortunately, there is some evidence for rapid adaptation (when evolutionary processes occur on ecological timescales), especially in species with short generation times[2,5,6]. Yet, it remains unclear whether most species have the capacity to adapt fast enough (particularly in complex environments that may constrain evolutionary responses[7,8]) and how evolutionary changes might affect community and ecosystem processes (particularly in dominant taxa). As a result, there is a need for targeted studies investigating evolutionary processes under natural environments in ecosystems worldwide[9]. We contend that global long-term ecological monitoring networks provide an unparalleled opportunity for such evolutionary inquiry.

Long-term ecological research networks (LTERNs) support research sites where environmental conditions and biological communities have been monitored for decades. Data collected at LTERNs have historically been used to investigate community and ecosystem dynamics and social–ecological processes, and to support environmental stewardship[10,11]. However, recent studies have demonstrated how these long-term ecological experiments can be successfully leveraged to address evolutionary questions (for example, examining whether increased nitrogen or long-term drought causes rapid adaptation of rhizobium mutualists[12] or primary producers[13]). In general, long-term

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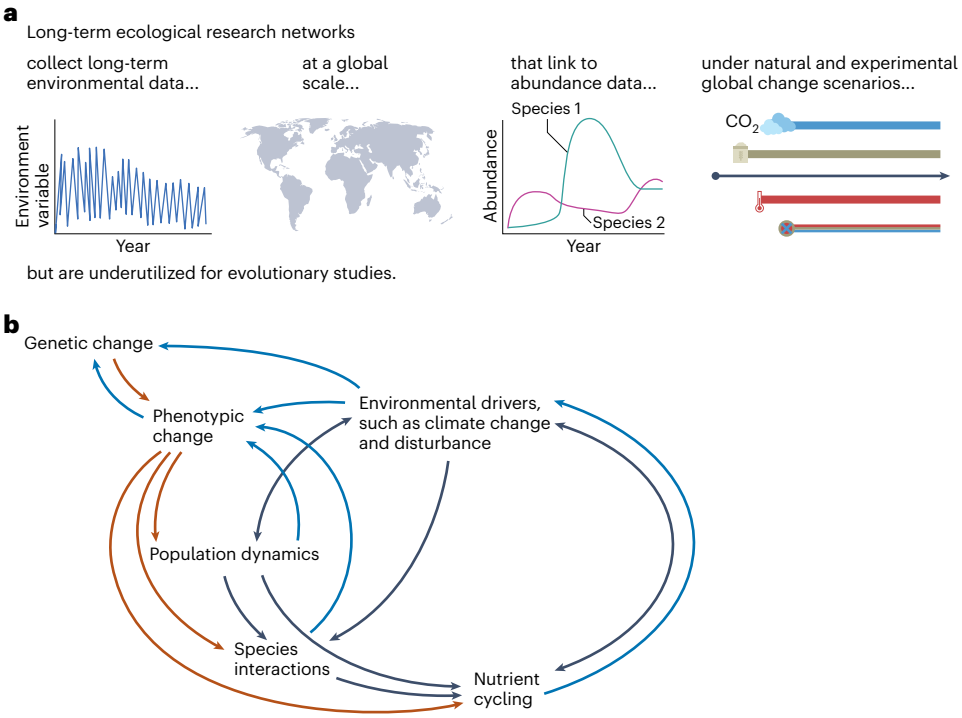

Fig. 1 | Global LTERNs provide unique opportunities to study the complex evolutionary patterns that are revealed over longer timescales. a, Leveraging LTERNs can help us to better understand the vital relationships between ecological processes, environmental changes and evolution. Such networks are currently underutilized for evolutionary studies, but can support our understanding of how species are simultaneously responding through ecological and evolutionary processes to global change. **b**, Schematic of ecological and evolutionary dynamics under global change. Leveraging these networks for evolutionary research can enhance the understanding of ecological dynamics and evolution under global change. The black arrows represent existing ecological relationships between common processes studied at global LTERNs, the red arrows represent evolutionary change affecting ecological processes and the blue arrows represent ecological or environmental change affecting evolutionary processes.

studies have established links between the environment and individual traits, genes and fitness[14–17] to document how natural populations are responding to environmental change[18–20]. Despite this, studies conducted at LTERNs rarely consider evolutionary questions.

Yet, these networks provide an important opportunity for evolutionary research because they: (1) span a huge variety of systems and species with diverse life histories in natural settings; (2) host ongoing, long-running experiments that can be harnessed to analyse drivers of evolutionary change; and (3) have extensive datasets on ecological and environmental conditions that comprise an excellent springboard for the pursuit of eco-evolutionary questions. For example, the International Long-Term Ecological Research Network includes more than 800 sites in various ecosystems (for example, grassland, temperate forest and marine) across 44 member countries where ecological data (for example, temperature, rainfall and abundance of focal species) have been gathered for up to five decades[21,22]. The Forest Global Earth Observatory Network includes over 77 sites across 29 countries that have collected data on forest function and diversity for the past four decades. These networks create extraordinary opportunities to examine the effects of global change on species, populations and communities (for example, ref. 23).

Although current ecological data collected over four to five decades may be insufficient for investigating evolutionary processes in longer-lived species, these data are certainly valuable when considering taxa with short generation times (insects, small mammals, many reptiles and amphibians, herbaceous plants and so on). This timeframe may also reveal evolutionary patterns such as gene flow or strong directional selection within longer-lived species. In addition, such time periods may help researchers to better understand how global change affects the direction and stochasticity of evolutionary change; for example, by capturing fluctuating selection (when the direction of selection changes over a relatively short time). We encourage researchers to explore the Dynamic Ecological Information Management System—Site and Dataset Registry (https://deims.org/), Environmental Data Initiative (https://edirepository.org/) and Forest Global Earth Observatory websites (https://forestgeo.si.edu/) to better understand the extent of available site-specific, open-source ecological data, species lists and resources and facilities.

In this Perspective, we address how LTERNs can help researchers to unravel the interconnected ecological and evolutionary processes driving species responses to global change (Fig. 1). First, we provide guidance on expanding long-term ecological experiments to address evolutionary questions that we specifically believe ecologists will find useful. Importantly, LTERNs provide unique opportunities to integrate ecology and evolutionary biology, as evolutionary processes undoubtedly affect the ecological patterns observed across LTERN sites (and vice versa) (Fig. 1). Second, we hope to familiarize researchers with the exciting opportunities that global LTERNs offer by illustrating how commonly collected data can be leveraged for new evolutionary insights. Third, we wish to call attention to barriers historically hindering evolutionary work within LTERNs. Ultimately, we intend to highlight how these networks can be used to advance our understanding of evolutionary responses to global change.

Expanding long-term ecological experiments for evolutionary insights

To understand evolutionary patterns, we must evaluate whether phenotypic change arises due to adaptive evolution (evolution that confers a fitness advantage in the context of selective pressures), non-adaptive evolution (evolution due to random processes such as

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BOX 1

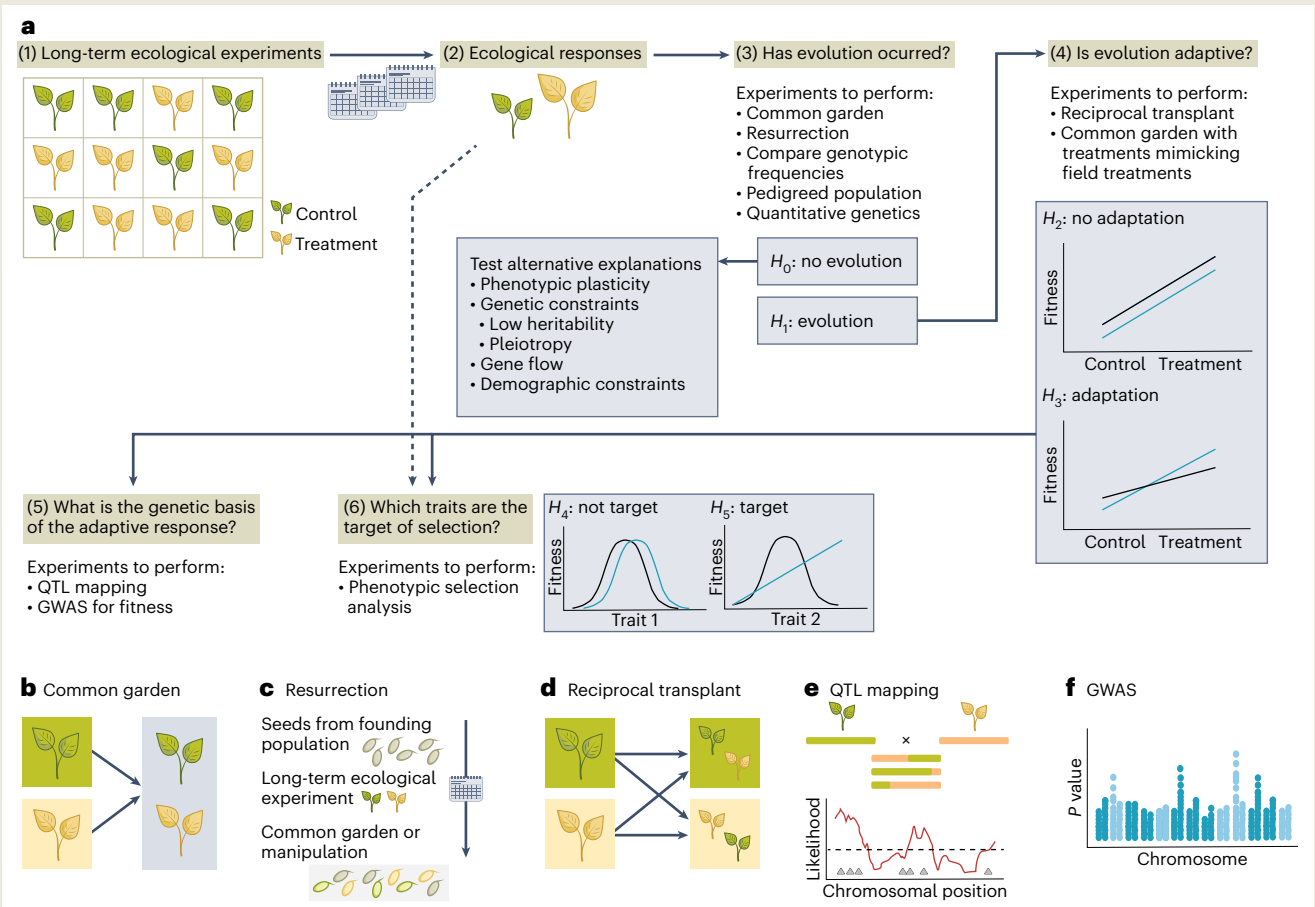
A framework for leveraging long-term ecological research to answer evolutionary questions

Many long-term ecological experiments at LTERNs involve decades of manipulation in replicate plots (for example, nitrogen addition or precipitation addition or removal). Researchers may be motivated to test for rapid evolution when they observe different phenotypic responses of the same species to alternative treatments. Researchers may also pursue evolutionary questions based on other theoretical or empirical knowledge (for example, one predicts that severe drought selects for trait values that confer drought avoidance or tolerance). It is important to emphasize that although the following methods do not require LTERNs, long-term experimental plots associated with LTERNs provide researchers with invaluable information and resources, including (but not limited to) plot history, detailed data on microhabitats and species, local knowledge on abiotic and biotic conditions from site managers and, crucially, the chance for comprehensive experimental results to be obtained through repeated measurements both within and across sites.

We highlight two possible paths that researchers might take to explore evolutionary dynamics at LTERNs. The entire sequence of inference in the diagram may not be necessary for every situation. For example, dissecting the genetic basis of adaptation is largely irrelevant to questions about whether evolutionary change feeds back to influence community structure and ecosystem processes.

In the first path (solid arrows), a researcher begins by testing whether potential phenotypic differences (panel **a**, step 2) have a heritable genetic basis and whether evolution has occurred (panel **a**, step 3). This hypothesis can be tested using a common garden experiment (panel **b**) to ask whether the mean phenotype from each treatment differs for organisms that were sourced from different treatments. Ideally, one should standardize maternal environmental effects by growing organisms for one generation in a common garden before the test generation. This step is also necessary for resurrection experiments (panel **c**). If desired, information on the quantitative genetic basis of phenotypic variation can be collected using pedigreed populations created through crosses. When phenotypic differences observed in the field do not persist in a common garden experiment, these differences probably reflect phenotypic plasticity. When researchers do not initially observe phenotypic differences, it may be valuable to test alternative explanations (panel **a**, step 3) to ask which factors may have impeded rapid evolution (for example, a lack of heritable genetic variation, gene flow through space or time or genetic constraints).

Evidence of evolutionary change does not necessarily imply that phenotypic change has been adaptive. In some situations, gene flow, genetic drift or limited genetic variation restrict adaptive responses to treatments. Therefore, further experiments would be needed to test whether evolutionary change confers a fitness advantage (panel **a**, step 4). However, when consistent evolutionary changes are observed across multiple replicate treatment plots, researchers



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could infer that selection probably underlies parallel evolution (although it is possible that replicated phenotypic evolution is due to mutational bias coupled with strong drift induced by an experimental treatment)[70]. To test for local adaptation, one must reciprocally expose a sample of genotypes sourced from each treatment plot or environment to all treatment conditions. Ideally, reciprocal transplants (panel **d**) are performed in the same field plots and under the same environment when permitted. Alternatively, one might grow organisms at another LTERN site or under a controlled environment where the original long-term treatments are simulated (for example, drought versus control treatments in a greenhouse).

Although a reciprocal transplant experiment can test whether evolutionary change is adaptive, it does not identify the traits that have been the targets of selection (panel **a**, steps 5 and 6). In the second path (dashed arrow), a researcher may begin by asking whether alternative environments differentially select for traits. The classical approach for identifying traits under selection is to relate fitness components to trait variation under different environments or treatments using selection analyses[71–73] (panel **a**, step 6). This approach is most effective when trait variation is manipulated (for example, expansion of trait variance) and when genotypes are replicated within a randomized design. We urge caution when attributing selection or adaptation to particular traits, as genetic correlations between traits due to pleiotropy or tight linkage may confound inferences of the targets of selection.

Molecular approaches such as QTL mapping (panel **e**), population genomic outlier analyses or genome-wide association studies (GWASs; panel **f**) can identify regions of the genome and candidate loci associated with traits subject to selection (panel **a**, step 5). Additionally, in cases where researchers have hypotheses about the alleles involved in adaptation to environmental factors (for example, from large-scale environmental association analyses), LTERN experiments can be used to retrospectively validate whether such alleles have changed in frequency (relative to controls) in plots that have been experimentally manipulated on those environmental axes.

mutation, recombination or genetic drift) or phenotypic plasticity (phenotypic variation resulting from environmental effects on trait expression). Additionally, an important component is understanding whether plasticity is adaptive or not[24]. As a first step towards determining whether evolution has occurred in response to components of global change, researchers can expand on long-term field experiments that are a hallmark of LTERN sites (for example, refs. 25–27). The most common ecological processes studied at LTERNs include nutrient cycling, primary production, disturbance and population and community dynamics (Fig. 1).

Researchers can collect individuals from treatment and/or control groups and use experimental approaches to assess whether phenotypic differences result from plasticity or evolution (Box 1a). For example, researchers capitalized on a long-term (22 years) LTERN experiment by using a common garden experiment (Box 1b) to demonstrate the evolution of less mutualistic *Rhizobium* strains in response to elevated nitrogen levels[12]. Other studies have used genotyping-by-sequencing in populations undergoing long-term treatments to reveal rapid evolution and reduced genetic diversity; for instance, in black grama grass (*Bouteloua eriopoda*) under drought conditions[13] and in the common reed (*Phragmites australis*) under increased nitrogen[28]. Resurrection experiments (Box 1c) can be used to compare the fitness and phenotypic traits of historical and contemporary lineages and rely on species having a dormant egg or seed stage. Such species are well represented across global LTERNs and have proved fruitful for evolutionary insights (for example, refs. 29–31). Reciprocal transplant experiments (Box 1d) or common garden experiments under natural conditions[32] can determine whether experimental populations have adapted to manipulated global change factors, as can resurrection methods in combination with a reciprocal transplant design[33]. Cross-site LTERN investigations would particularly benefit these types of studies, specifically when researchers are interested in dominant, generalist or invasive species that can be found across LTERN sites comprising similar ecosystems (see https://deims.org/, where a researcher can search for specific ecosystems or choose observed properties and all relevant sites and the affiliated network will be listed). Common gardens, reciprocal transplants and resurrection experiments can also be used to discern the effect of phenotypically differentiated populations on ecological processes and ecosystem parameters for researchers interested in feedback loops and how evolutionary change shapes ecological processes (Fig. 1).

In cases where long-term studies lack a control, researchers can use unassociated reference plots at each site to account for site-specific random effects (for example, ref. 34). Although this can also apply to long-term studies conducted outside of LTERN sites, using long-term experimental plots associated with LTERNs is valuable because researchers have access to: (1) information on plot history (for example, treatment timing, effect size and so on); (2) high-resolution microhabitat and species data that are otherwise unrepresented in global temperature datasets and species distribution models; and (3) repeated measures via replicate plots both within and across sites.

Quantitative trait loci (QTL) mapping (Box 1e) and genome-wide association studies (Box 1f) can reveal genomic changes linked to traits and fitness shifts in long-term treatment and control groups. For example, researchers used QTL mapping to uncover the major loci influencing adaptation in two grass ecotypes physiologically adapted to different ecosystems within LTERN sites[35]. Researchers should avoid concluding an adaptive response from molecular studies alone because differences may be attributed to non-adaptive or neutral evolution (evolution due to the accumulation of mutations that do not provide a selective advantage or disadvantage)[36]. However, combining genomic techniques with the experimental approaches described above can be extremely powerful for linking the genomic basis of adaptation across space and time to phenotypes, community shifts and ecosystem functions (for example, refs. 37,38).

Leveraging long-term data for novel evolutionary insights

Applying these classic approaches in LTERN studies might be particularly powerful given that long-term ecological changes are already well documented in many LTERN sites[11]—providing an opportunity to investigate the effects of changing ecological patterns on evolution. To familiarize scientists with LTERNs, we propose examples of evolutionary questions motivated by existing LTERN studies (Fig. 2). Most ongoing LTERN studies focus on the ecological impacts of altered nutrient fluxes, bioinvasions, environmental disturbances, extreme climatic events or changes to community structure or primary production. These ecological patterns may alter the evolution of component populations and can therefore be used to address questions about how ecological pressures affect evolution, and reciprocally how evolutionary responses may influence ecological outcomes.

Opportunities to study evolution under natural environments

Performing evolutionary experiments in laboratory settings or semi-natural environments allows researchers to isolate the effect of one or a few environmental variables on fitness and trait expression[39,40]. Yet, it does not account for the complex and covarying factors that are inherent in nature and are perhaps the most important influences on

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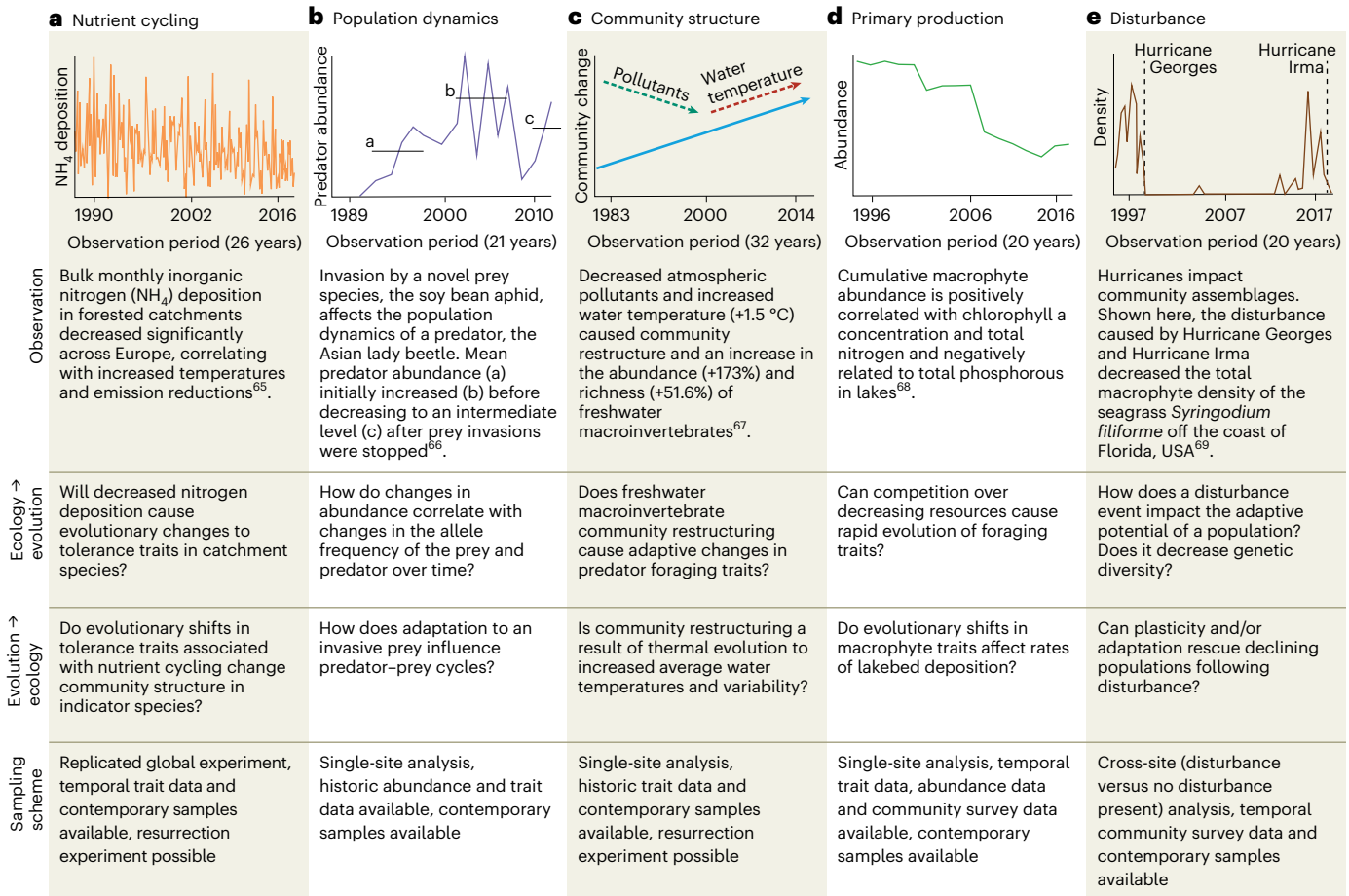

Fig. 2 | Examples of published studies from global LTERNs and potential evolutionary inquiries. Existing, long-term ecological studies provide unique opportunities for collaboration among ecologists and evolutionary biologists to evaluate ecological dynamics and evolution under global change. **a**–**e**, Here we present the results of published studies from various LTERN sites around the globe that investigated how changing environmental conditions, including nutrient cycling[65] (**a**), changes to population dynamics[66] (**b**), community structure[67] (**c**), primary production[68] (**d**) and disturbance[69] (**e**), affect ecosystem processes. These have been included as they are common overarching themes across many LTERNs. We propose questions specific to these themes that researchers can ask as an extension to existing studies. Additional research can focus on how ecological or environmental change is affecting evolutionary processes (ecology → evolution) or how evolution is affecting ecological processes (evolution → ecology). Information on potential sampling schemes and available data that can be used to address questions is also presented. Credit: **a**, adapted with permission from ref. 65, Elsevier; **b**, adapted with permission from ref. 66, American Institute of Biological Sciences; **c**, adapted with permission from ref. 67, Elsevier; **d**, adapted from ref. 68, Springer Nature; **e**, adapted from ref. 69, Springer Nature.

eco-evolutionary dynamics and outcomes[41–43]. Importantly, we urge researchers to consider global LTERNs as a valuable resource for studying evolution in the real world because: (1) the infrastructure to perform field studies in natural environments already exists (for example, laboratories, field stations and treatment plots); and (2) an existing community of researchers can provide knowledge on how best to conduct complex experiments specific to each site when considering site-specific problems (flooding, biotic interruptions and so on). Engaging with local researchers is also important when considering that many sites have intricate plot histories, where treatments may have changed over time due to the need to secure long-term funding. To secure ongoing support, researchers may need to explore new questions and introduce additional treatments. Yet, this challenge underscores an advantage of LTERNs over other research locations for those considering long-term studies. These networks provide access to extensive records and the expertise of researchers familiar with plot history.

We would also like to highlight additional infrastructures such as the Nutrient Network (https://nutnet.org/), FLUXNET (https://fluxnet.org/), the International Drought Experiment (https://drought-net.weebly.com/) and the Disturbance and Resources Across Global Grasslands Network (https://nutnet.org/dragnet). These networks support global, long-term experiments with standardized protocols, allowing for increased precision and inference about evolutionary dynamics under natural conditions. Importantly, these initiatives are driven by voluntary participation and researchers are encouraged to propose add-on measurements to their often simple designs, affording a straightforward mechanism to the inclusion of evolutionary research[44]. Additional information on research initiatives, parameters observed, biomes represented and the number of sites and countries participating in each LTERN mentioned here can be found in Supplementary Table 1.

Overcoming limitations of global LTERNs

Despite their utility for answering evolutionary questions, few evolutionary studies have been conducted at LTERNs. Here we address obstacles hindering evolutionary work at LTERNs and offer suggestions to overcome them.

Focal species studies

Studies at LTERN sites tend to focus on individual species that are ecologically important, such as dominant plant species that mediate ecosystem function or are of conservation interest. For example, *Spartina alterniflora* is well studied in coastal LTERNs given its global distribution

and role as an ecosystem engineer[45,46]. Although this limitation may restrict researchers studying non-focal species, it also renders LTERN sites highly suitable for studying evolution in focal species. Indeed, because many focal species are clonal plants and long-term experiments may retain source propagules, these species are amenable to the manipulative approaches we discussed earlier, including common garden studies, reciprocal transplants and resurrection experiments. Researchers interested in leveraging LTERN studies focusing on dominant species should be mindful that manipulated plots may only contain a fraction of the total population. If these plots constitute a small portion of the overall population, gene flow may dilute evolutionary responses to ecological manipulations (but see ref. 47 for a discussion on microgeographic adaptation).

In the future, we argue that LTERNs should strategically begin archiving genetic material (for example, ref. 48) and recording phenotypic data (through photographic records or surveys) for ecologically important species. Although some sites may already record phenotypic data for certain species, the sampling scheme is often determined by the need of an individual study. An organized, multi-site endeavour would benefit all researchers. For example, the Disturbance and Resources Across Global Grasslands Network recommends that all participating sites start a seed bank, where propagules are collected and stored from both treatment and control plots. Soil microbiomes (and when appropriate, microbiomes specific to other species, such as skin microbiomes in amphibians) should also be considered for archiving, and cultures of infectious pathogens could be considered for cryopreservation. LTERN managers should consult evolutionary geneticists or other relevant experts for advice on archiving schemes (for example, the number of samples, time span between samples and so on).

Single-site studies

Most studies at LTERNs include experiments or long-term data collected at a single site, probably because of the logistical difficulties of setting up, conducting and coordinating across-site experiments. We have discussed how in situ experiments such as reciprocal transplants should be considered across sites. However, we urge researchers and network managers to collaborate on identifying additional strategies to maximize data output for evolutionary insights. For example, sites that comprise similar ecosystems could start collecting individual-level data (trait data and genetic material) on the same species or species of the same functional group. By having data replicated across sites, researchers could potentially identify where natural selection has resulted (or not) in parallel evolution. Given that many species of plants and animals are advancing their phenological transitions in response to climate change[49–51], we suggest that researchers consider monitoring phenology as a key trait in these new endeavours. When a disturbance or bioinvasion occurs exclusively at one site, genetic and ecological data will be available at other locations that have not been affected. For example, the National Ecological Observatory Network performs coordinated collection of abiotic and phenology data across sites in the USA that could be leveraged to examine the consequences of disturbance and to monitor invasion fronts.

Lack of genetic reference material

Assembled genetic material, in the form of reference genomes and transcriptomes, has not yet become a research focus for LTERNs. Although many well-tested and reference-free approaches for analysing genetic data are available (such as reduced representation methods), these methods still present challenges for species with complex genetic structure, such as mixed polyploidy, and/or large genomes. Expanding methods for analysing polyploid genetic data are promising[52,53], as are the declining costs of sequencing and ongoing interdisciplinary collaborations aimed at producing high-quality reference genomes. For example, a large team recently created a high-quality switchgrass genome assembly to understand its adaptation to climate, despite its large and complex genome[54]. This resource will make it easier for future researchers to detect variation, monitor change and investigate gene function in this key species. We call for targeted funding programmes to create similar genomic resources for ecologically important non-model organisms in LTERNs.

Geographical gaps

The distribution of long-term studies tends to bias towards Northern Hemisphere ecosystems[55]. If researchers are to truly understand the long-term effect of global change on the world's biodiversity and ecosystems, there needs to be a wider range and higher coverage of LTERN sites across a greater diversity of ecosystems. Accomplishing this expansion across political borders is challenging, particularly when considering the scope of funding needed to establish and maintain sites. It is fundamental that networks support programmes such as match-funding schemes across nations and incentivize collaborative efforts[56].

Awareness in the evolutionary biology community

In general, the fields of ecology and evolutionary biology may often be siloed and there is no exception to this within the LTERN community. Network managers and researchers familiar with LTERNs should encourage collaborative eco-evolutionary work by widely distributing network newsletters, attending evolution-focused conferences and planning dedicated sessions at interdisciplinary meetings to facilitate conversations and raise awareness on the exciting opportunities LTERNs present for evolutionary work.

Social and financial constraints

Dismantling social barriers that prevent individuals from conducting evolutionary research at LTERN sites is imperative to productive investigations. First, creating an equitable, inclusive, safe and welcoming environment for fieldwork for all researchers is of the utmost importance[57–60]. Second, ecologists and evolutionary biologists must improve their collaborative efforts across disciplines, sites and countries to capitalize on global LTERNs. Collaborations with local communities and/or Indigenous people in the areas of research, as holders of long-term knowledge, will serve to enhance efforts. Third, seasoned LTERN investigators should provide opportunities for early-career evolutionary researchers to become involved in long-term projects. Investigators will benefit from the diverse perspectives of early-career researchers and cross-disciplinary collaborations will support new evolutionary research.

Early-career researchers may hesitate to pursue long-term research because of the pressure to publish frequently in academia. However, LTERNs mitigate this barrier by providing early-career and under-represented researchers access to long-term funding, rich longitudinal datasets, well-developed experimental infrastructure and extensive knowledge about local ecosystems. Although early-career researchers may be dissuaded from long-term research because their careers require them to move institutions often, LTERNs provide opportunities for research regardless of affiliation.

To further the goals of this Perspective, we encourage funding organizations to consider additional support for evolutionary studies at LTERNs. Specifically, funding agencies should consider establishing a dedicated funding scheme explicit to supporting research addressing evolutionary questions at LTERNs, with an emphasis on international collaborations. This could be a new funding programme that is parallel or similar to the Long Term Research in Environmental Biology Program from the US National Science Foundation. Targeted funding programmes can help to overcome limitations posed by the costs of archiving and organizing samples, preserving tissue samples for genomic analyses and conducting bioinformatics studies, in addition to evolutionary experiments.

Top four priorities moving forward

We suggest four actions to increase evolutionary work at LTERN sites:

(1) We encourage ecologists to record individual-level trait and fitness/performance data in ongoing and new experiments at LTERN sites. Researchers may consider archiving samples for genomic studies, as well as maintaining a collection of resting life stages of relevant species (such as seed banks).

(2) We suggest that evolutionary biologists inquire with data managers as to what types of studies and data are available at global networks and to look at existing data repositories.

(3) We encourage network managers to publish and broadly distribute quarterly newsletters on recently published studies, facilitate network-wide mixed conferences that include evolutionary biologists and set up baseline species trait and genetic material data repositories.

(4) We call for funding agencies to allocate more resources to programmes that support long-term experiments focused on evolution, such as the National Science Foundation's Long Term Research in Environmental Biology Program, and to consider creating additional dedicated funding programmes for long-term evolutionary research. Moreover, increased cross-site studies, including international collaborations, should be a priority.

Concluding remarks

Recent reviews highlight the importance of long-term ecological monitoring networks for ecological insights[10,11,21,61] but overlook the opportunity that networks present for understanding evolutionary responses to environmental change[62,63]. The percentage of evolutionary studies that occur at such sites is low[10] and recognition among ecologists and evolutionary biologists that long-term ecological networks are ideally suited for addressing species' evolutionary responses to climate change is limited[64].

Here we have outlined how global LTERNs' infrastructure and data can be used to investigate species' evolutionary responses to climate change (Box 1). Additionally, we offer examples of recent studies from global LTERN sites that can inspire new evolutionary inquiries (Fig. 2) and we propose priorities for researchers, network managers and funding agencies moving forward. Most importantly, we believe that global LTERNs are valuable beyond the long-term data they provide. They also establish a foundation where researchers across institutions, disciplines and countries can foster new collaborations and instil future generations of ecologists and evolutionary biologists the value of long-term research for evolutionary insights.

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Competing interests

The authors declare no competing interests.

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