

Long-term research in ecology and evolution: a survey of challenges and opportunities

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Abstract. Long-term research in ecology and evolution (LTREE) is considered fundamental for understanding complex ecological and evolutionary dynamics. However, others have argued for revision of LTREE efforts given perceived limitations in current research priorities and approaches. Yet most arguments about the benefits and failings of LTREE could be argued to reflect the views of only the limited number of scientists who have authored reports on the field, and not the wider community of ecological and evolutionary scientists. To more systematically and quantitatively assess the views of the community on LTREE contributions and future activities, we conducted and here report the results of a survey of ecological and evolutionary scientists at primarily U.S.-based institutions, completed by 1,179 respondents. The survey objectives were to (1) identify and prioritize research questions that are important to address through long-term, ecological field experiments and (2) understand the role that these experiments might play in generating and applying ecological and evolutionary knowledge. Almost 80% ($n = 936$) of respondents said that long-term experiments had contributed “a great deal” to ecological understanding. Compared to other research approaches (e.g., short-term, single-site, modeling, or lab), there was overwhelming support that multi-site, long-term research was very important for advancing theory, and that both observational and experimental approaches were required. Respondents identified a wide range of research questions for LTREE to address. The most common topic was the impact of global change ($n = 1,352$), likely because these processes play out over many years, requiring LTREE approaches to fully understand. Another recurrent theme was the potential of LTREE approaches to build evolutionary understanding across all levels of ecological organization. Critical obstacles preventing some scientists from engaging in LTREE included short-term funding mechanisms and fewer publications, whereas the longer-term value for advancing knowledge and an individual’s career were widely recognized. Substantive advances in understanding ecological and evolutionary dynamics then seem likely to be made through engagement in long-term observational and experimental research. However, wider engagement seems dependent on a more supportive research environment and funding structure, through increased institutional acknowledgement of the contributions of long-term research, and greater program support during the establishment and maintenance of research.

Key words: community; ecosystem; evolution; experiment; future challenges; long-term ecological research; observation; population; review; survey; theory.

INTRODUCTION

Long-term research in ecology and evolution (LTREE) is considered fundamental for testing and developing theory, and for understanding complex ecological and evolutionary patterns that often emerge only over longer time scales (Turner et al. 2003, Silvertown et al. 2008, Ducklow et al. 2009, Clutton-Brock and Sheldon 2010, Magurran 2010, Hughes et al. 2017). Not surprisingly then, the necessity and value of long-term research is often lauded by researchers and funding agencies (Callahan 1984, U.S. Long Term Ecological Research Network [LTER] 2007, Michaels and Power 2015). However,

others have suggested the need to revise current LTREE designs because of gaps in research priorities (U.S. Long Term Ecological Research Network [LTER] 2007), opportunities for expansion into underrepresented fields (Dunne et al. 2004, Müller et al. 2010, Ohl and Swinton 2010, Brodersen and Seehausen 2014), and limitations of current long-term experimental designs and data collection strategies (Lindenmayer and Likens 2009, Lindenmayer et al. 2010, Peters 2010). Yet most debates on the benefits and failings of LTREE activities could be argued to reflect the views of only the limited number of scientists who have authored reports on the field, and not the wider community of ecological and evolutionary scientists.

In the United States, perhaps the best-known and most well-funded LTREE program is the National Science Foundation’s Long-Term Ecological Research Program

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(Magnuson 1990, Hobbie 2003, U.S. Long Term Ecological Research Network [LTER] 2007, Michaels and Power 2015). Its original and continuing focus on five core research areas, namely primary production, population studies, movement of organic matter, movement of inorganic matter, and disturbance, means that LTER research has primarily focused on community and ecosystem ecology (Callahan 1984). It has been argued that the LTER program has generated significant advances in these two fields (Magnuson 1990, Hobbie 2003, Michaels and Power 2015), but that these advances may have come at the cost of a more synthetic knowledge that could have been generated by the integration of fields like evolutionary biology (Brodersen and Seehausen 2014) or those in the social sciences (Redman et al. 2004, Müller et al. 2010, Ohl and Swinton 2010, Collins et al. 2011, Michaels and Power 2015). One mechanism to further such discussion on the future of LTREE initiatives is to gather community-wide perspectives on the research approaches that will most advance understanding of ecological and evolutionary dynamics.

Ecological data is frequently binned into a suite of binary categories—long vs. short, observational vs. experimental, multi-site vs. single-site—and each is argued to have unique advantages and limitations (Krebs 1991, Peters 2010). A formal analysis of how the community views the relative merits of different categorizations of research for objectives such as advancing understanding, might help structure the design of future LTREE initiatives. Current LTREE initiatives span a range of possibilities. For example, the LTER program has historically focused on single-site, experimental research (Callahan 1984, Peters 2010). Conversely, the new National Ecological Observatory Network (NEON) in the United States focuses on multi-site, observational (i.e., monitoring) data collection (Schimel et al. 2007). Other U.S. federally funded long-term research, such as the Forest Inventory and Analysis, and private initiatives such as the U.S. National Phenological Network or the Audubon Christmas Bird Count also focus on multi-site, observational data but for a more narrow set of parameters (Butcher et al. 1990, Bechtold and Patterson 2005, Müller et al. 2010, Schwartz et al. 2012). Bottom-up efforts have led to the emergence of multi-site, experimental studies, such as the Nutrient Network (Adler et al. 2011) or the Global Invasive Impact Network (Barney et al. 2015), which given their success are evolving from short- to long-term studies. There have been calls to proactively design LTREE initiatives that bridge these various long-term research models (Krebs 1991, Müller et al. 2010, Peters 2010, Michaels and Power 2015). Surveying community views on the relative merits of the different models and short and long-term research can contribute to the effort to prioritize the design of future LTREE research and funding.

We analyze responses from the Long-Term Ecological and Evolutionary Research Survey (Bradford et al. 2017), which was an assessment targeted at understanding the

views of primarily U.S.-based scientists in the ecology and evolutionary biology fields on long-term ecological research. The survey was designed to be broadly inclusive of the ecological and evolutionary biology research communities and was completed by over 1,000 scientists. The primary objectives of the survey were to help (1) identify and prioritize research questions that are important to address through long-term, ecological field experiments (including those considering evolutionary effects and responses) and (2) understand the role that these experiments might play, as part of a broader set of approaches, in generating and applying ecological and evolutionary knowledge. Key findings from the survey include (1) the past and current contributions of LTREE, (2) its role in the development of theory and understanding relative to other approaches, (3) important topics and questions for LTREE to address, and (4) barriers and incentives to LTREE.

METHODS

Survey development and deployment

The survey questionnaire and method (e.g., distribution and deployment) was developed adhering to the standards of the American Association for Public Opinion Research, in consultation with the Yale Program on Climate Change Communication. It was administered online using Qualtrics Survey Software (Qualtrics, ???, ???, USA) under site license to Yale University. The questionnaire and respondent data are archived and freely available (Bradford et al. 2017). Survey creation was a multi-step process, with questions and format developed and then revised with input from an external advisory committee comprising senior and junior ecological and evolutionary researchers in the United States (see *Acknowledgments*). The advisory committee comprised individuals from both within and external to existing long-term research networks. The survey was further revised after beta testing by administering to ~100 ecological and evolutionary scientists.

The final questionnaire was soft-released (i.e., distributed to ~100 academic colleagues) to ensure that it was working and then fielded two days later (7 January 2015). Two professional societies agreed to distribute it to their membership. Each society, the Ecological Society of America (ESA) and the American Society of Naturalists (ASN), sent out three emails to all of their members to ask them to take the questionnaire. The initial invitation email was followed-up approximately 1 week later with a reminder and again after 2 weeks with a final reminder. The questionnaire was available online through 8 February 2015. The ESA has over 10,000 members and is the largest ecological society in the United States. The ASN has approximately 1,200 members and is focused on advancing understanding of evolution, ecology, and behavior. As such, the questionnaire was circulated to a large number of practicing ecologists and a smaller proportion of evolutionary scientists. More evolution specific

1 societies were unable to distribute the questionnaire at the
2 time asked. As such, the questionnaire was also posted to
3 three list servers, the National Science Foundation's
4 (NSF) Long-Term Ecological Research Network, the
5 University of Maryland's ECOLOG-L, and McMasters
6 University's Evolution Directory (EvolDir). The distribu-
7 tion approach intentionally targeted practicing ecologists
8 and evolutionary biologists in the United States, but any
9 responses from scientists affiliated with non-U.S. institu-
10 tions were retained. Given the use of list servers the
11 response rate is difficult to gauge specifically, but taking
12 only the society membership and (falsely) assuming that
13 scientists belong only to ESA or ASN, suggests a response
14 rate of ~10% (i.e., 1,179 respondents of ~11,800 members
15 emailed). Further, the distribution primarily targeted U.S.
16 scientists, and so the results likely most apply to U.S. insti-
17 tutions and funding agencies, but scientists' perspectives
18 on the contributions and potential of LTREE science
19 presumably extend beyond national borders.

20 The survey included both quantitative and qualitative
21 questions. Quantitative (both ordinal and categorical)
22 closed-ended questions used a pre-defined set of response
23 categories, facilitating direct comparison across all respon-
24 dents. Qualitative, open-ended questions, by contrast, pro-
25 vided respondents the opportunity to develop their own
26 answers, potentially in unexpected directions, providing
27 richer insights, but with more subjective analysis. Specifi-
28 cally, we employed quantitative questions to score views
29 on the extent to which long-term experimental research
30 has contributed to understanding in ecology and evolu-
31 tionary biology; its role compared to other approaches
32 (e.g., short-term experiments); justifications for and
33 caveats to long-term experiments; and the relative impor-
34 tance of incentives for conducting long-term research.
35 Respondents were given the opportunity to expand on
36 their answers through open-ended qualitative questions,
37 which also were designed to assess community views on
38 the most important topics and questions for long-term
39 research to address (Appendix S1: Table S1 and Data S1),
40 and primary incentives (Appendix S1: Table S2 and Data
41 S1) and challenges (Appendix S1: Table S3 and Data S1)
42 to realizing this work. Lastly, we collected demographic
43 data to determine if views were conditional on such things
44 as years of experience and field of expertise.

45 We provided the following operational definitions: An
46 "experiment" is a deliberate manipulation of a variable or
47 variables to understand the effects on a system or aspects
48 of the system (e.g., populations or biogeochemical cycles).
49 By contrast, "natural experiments" or "gradients"—such
50 as hurricanes, oil spills, or spatial variation in climate—
51 were defined as "observational," as were other approaches
52 that do not involve direct manipulation by the investiga-
53 tor of a putative controlling variable (e.g., monitoring).
54 "Long-term" described research for durations greater
55 than 5 yr. We acknowledged that in some systems, for
56 example, where species have rapid population turnover
57 times, "long-term" might be viewed from the context of
58 number of generations as opposed to time.

Data analysis

Closed-ended questions were primarily analyzed by cal-
culating the proportion of the total number of the ques-
tionnaire takers ($n = 1,179$) who selected a pre-defined
response. For some questions, we used additional statisti-
cal techniques to test for trends. For example, we asked
respondents to compare the role of short-term and long-
term research at both single sites and multiple sites to the
development of general ecological theory. To assess
responses, we used the Wilcoxon signed-rank test, a non-
parametric test useful for comparing related samples from
the same population. The non-parametric test was chosen
over the more common paired t test due to the ordinal
data (Likert-scale items) collected in this set of questions.

For open-ended questions, thematic coding was used to
categorize and analyze responses. Thematic coding is an
inductive process by which key concepts and ideas are
defined as themes, which can be identified and aligned
within a larger set of responses (Braun and Clarke 2006).
Following coding, we qualitatively analyzed question-
naire responses to identify major questions to be
addressed through long-term research, opportunities for
future research, and barriers to conducting that research
(Appendix S1: Data S1). We also used quantitative
approaches to identify trends in responses to open-ended
questions based on the demographics of respondents and
opinions about various aspects of long-term ecological
research. Specifically, we used binary logistic regression
to test for the impact of years of experience, area of spe-
cialization, research network involvement, and PhD type
on the likelihood of respondents giving various open-
ended responses (such as barriers or incentives for long-
term research). Most of these tests for connections
between respondent characteristics and responses were
insignificant and are not reported here. Quantitative and
statistical analyses were conducted using SPSS statistical
software (IBM SPSS Statistics for Windows, Version
22.0, Released 2013; IBM, Armonk, New York, USA).

Note that in reporting outcomes from the survey we
attempt to provide interpretations of the results that
reflect the community perspectives given. In the instances
where we offer our own interpretations apart from those
of the respondents, we endeavor to make this clear.

RESULTS AND DISCUSSION

Demographics of respondents

A total of 1,179 respondents completed the question-
naire. We collected demographic data in part to character-
ize the respondents and ensure that they were not
dominated by a particular sub-group of the wider ecologi-
cal and evolutionary community (e.g., those receiving
funding through large federal efforts such as the NSF
LTER program). This demographic assessment is particu-
larly important given the difficulty in obtaining a reliable
response rate owing to the sampling process we used.

Although ~60% of respondents ($n = 681$) were involved with LTREE projects, only ~20% were funded by the NSF LTER program ($n = 260$), with no other federal or state mechanisms funding more than ~5% of respondents. There was a gender imbalance, with nearly 60% of respondents identifying as male ($n = 700$) and just over one-third as female ($n = 430$). This imbalance may reflect skewed gender distributions in more senior ranks, given that respondents predominantly had many years (median=20.0 yr) of professional experience in ecological and/or evolutionary science, although more junior scientists were represented (one-fifth of respondents reported <5 yr experience). Over two-thirds of respondents were referred to the online questionnaire via a professional science organization ($n = 812$), with those referred through the Ecological Society of America ($n = 471$) most represented. The largest proportion of respondents identified their field of expertise as community ecology, followed by ecosystem ecology, plant ecology, aquatic ecology, and evolutionary ecology (Fig. 1). Reflecting the fact we targeted the U.S. research community, ~61% ($n = 716$) of respondents indicated that they were primarily based at U.S. institutions and an even greater proportion conducted field research within the U.S. ($n = 858$, 72%). Respondents did conduct field research on other continents ($n = 326$) and more than four-fifths ($n = 987$) described themselves as very or moderately familiar with LTREE research. Overall then, our respondents appeared to represent an experienced body of scientists that were associated with professional societies, familiar with LTREE research, and actively engaged in

field research both within and outside the United States. In terms of potential bias, there were more ecological scientists than evolutionary scientists in the sample population, and within ecologists the fields of community and ecosystem ecology were the most strongly represented (Fig. 1). Additionally, it is possible that scientists involved with LTREE research were more likely to complete our survey relative to scientists not involved with LTREE research, which may explain why the majority of respondents reported they were a part of LTREE research projects.

Contributions to understanding

Respondents placed a high value on the contributions of long-term ecological experiments to the generation of ecological and evolutionary understanding, although the contributions were considered strongest to ecological science. Specifically, almost 80% ($n = 936$) of respondents said that long-term ecological experiments had contributed “a great deal” to understanding in ecological science. By contrast, 59% of respondents said LTREE had contributed a great deal or a moderate amount to understanding of evolutionary science ($n = 695$) and evolutionary ecology ($n = 813$). Fewer than two percent of respondents said that long-term ecological experiments had not at all contributed at all to understanding in ecological science ($n = 2$), evolutionary science ($n = 23$), or evolutionary ecology ($n = 14$).

Among different sub-fields, however, there was large variation in the extent to which respondents said that

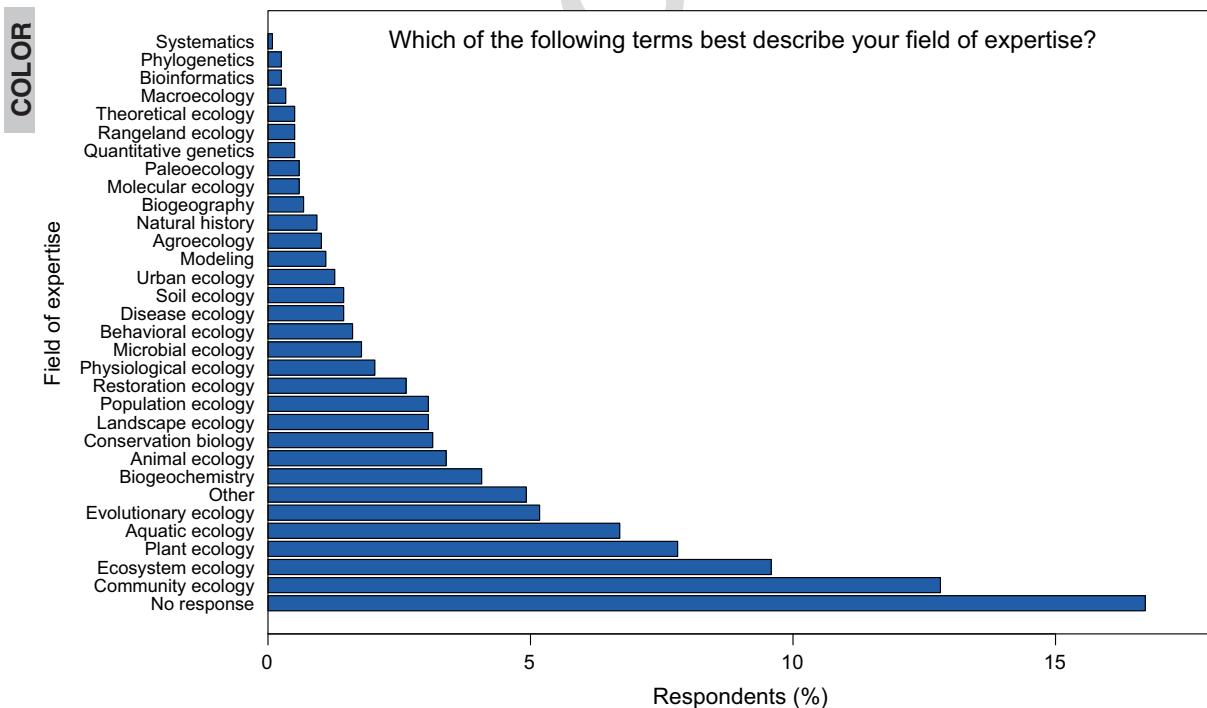


FIG. 1. Primary fields of expertise self-identified by 1,179 respondents to a questionnaire on long-term research in ecology and evolution.

1 long-term ecological experiments had contributed to
 2 scientific understanding (Fig. 2). Of 29 specific areas,
 3 more than one-half of the respondents felt that long-term
 4 experiments had contributed a great deal to the under-
 5 standing of ecosystem and community ecology, including
 6 nutrient cycling, succession, and global change effects
 7 (Fig. 2). These proportions declined to below 50% for
 8 topics in population ecology, to below 40% for landscape
 9 ecology, and to 20% or less for topics in evolutionary
 10 ecology (Fig. 2). We examined this pattern further to ask
 11 whether these varying contributions reflected the fact that

respondents were best represented by those with expertise
 in, and hence familiarity with, community and ecosystem
 ecology. For those who identified as experts in evolution-
 ary ecology, ~50% of the respondents felt that LTREE
 had contributed a great deal to evolutionary science and
 evolutionary ecology and none reported that they were
 unsure as to how LTREE had contributed to evolution-
 ary ecology (compared to 20% of respondents who identi-
 fied as experts in ecology). Overall then, these results
 likely indicate that long-term ecological experiments are
 best known (at least within our sample population) for

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How much would you say LTREE has contributed to our understanding of the following specific areas within ecological and evolutionary science?

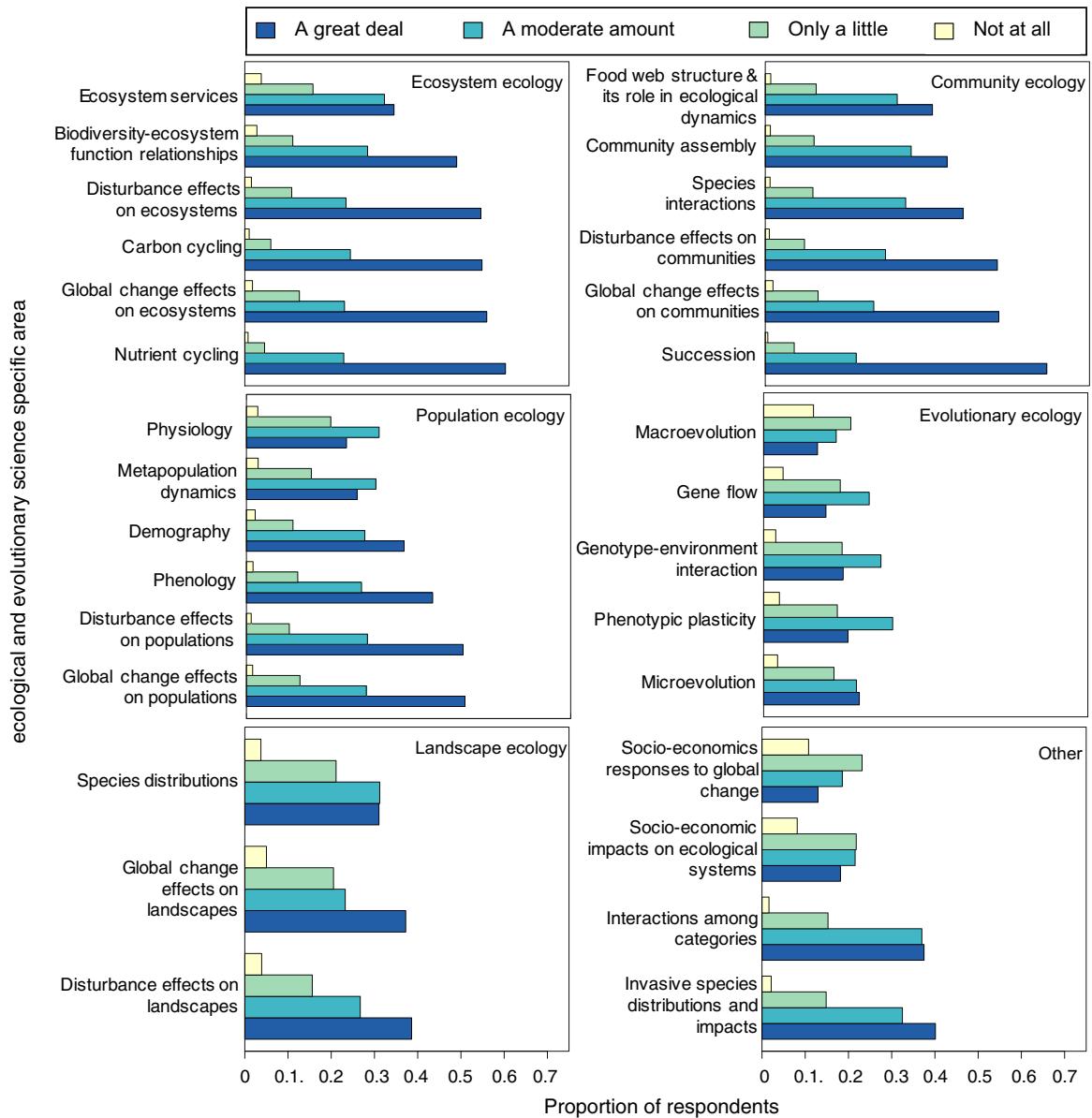


FIG. 2. Respondents ($n = 1,179$) to a questionnaire on long-term research in ecology and evolution (LTREE) felt that past and current LTREE had contributed most to knowledge within the subfields of ecosystem, community, and population ecology.

generating knowledge about community and ecosystem dynamics, but that they have similarly large potential to further knowledge in other areas such as evolutionary ecology that have been underrepresented in research efforts (Clutton-Brock and Sheldon 2010, Collins et al. 2011, Brodersen and Seehausen 2014). We suggest that the latter should be considered during planning of future LTREE initiatives in terms of opportunities for jointly advancing ecological and evolutionary understanding.

Role of long-term research approaches

We posed a series of questions designed to evaluate whether long-term experiments are thought to play a unique and important role in generating understanding of ecological and evolutionary patterns, and for developing general theories that apply across organisms and systems. Respondents overwhelmingly said that long-term experimental research was better equipped to address certain types of questions than short-term research. The strongest justification for using long-term experiments was reflected in the statement, “long-term changes to complex ecological systems are often unpredictable, highlighting the need for long-term study of responses to experimental manipulations.” Over 90% ($n = 1,089$) of respondents said this statement was “generally accurate” and nearly three-quarters of these respondents ($n = 783$) said that this was a very strong justification for long-term experiments. Further, well over three-quarters of respondents ($n = 962$) agreed that “short-term (<5 yr) experiments often quantify only the immediate and transient effects of perturbation.”

Notably, respondents generally believed that long-term experiments do not depreciate in value and are not too

logistically complex to conduct. Specifically, they rated the following statements as “generally inaccurate”: (1) “The value of long-term experiments diminishes as their duration increases, because newer experiments generate more understanding per unit of time and money invested” ($n = 997$, 85%); (2) “Informative long-term experiments are logistically impractical because multiple factors (i.e., more factors than an investigator can feasibly manipulate) influence the structure and functioning of complex ecological systems” ($n = 916$, 78%). There was less but still quite substantive support ($n = 754$ “generally accurate” responses, 64%) for the statement that, “only long-term experiments can identify the mechanisms/processes that occur over longer time scales (e.g., community shifts, adaptation) that are necessary for predicting the responses of complex ecological systems.” Of those respondents who said this statement was generally accurate, almost three-quarters said this was a very strong ($n = 528$) justification for conducting long-term experiments. We were surprised by this level of support for long-term experiments in terms of the majority rejection of caveats, such as depreciating value and logistic impracticality, primarily because these community views run counter to some arguments made for discontinuing long-term work when it comes to the allocation of limited funding dollars (Legg and Nagy 2006, Lindenmayer and Likens 2009, Hughes et al. 2017). The survey results therefore indicate strong support for the continuation of long-term experiments for advancing ecological and evolutionary understanding.

The perceived value of long-term research for developing general theory was, however, strongly dependent on whether the experiments were conducted at single or multiple sites, but unaffected by whether the work was experimental or observational (Fig. 3). Specifically, respondents

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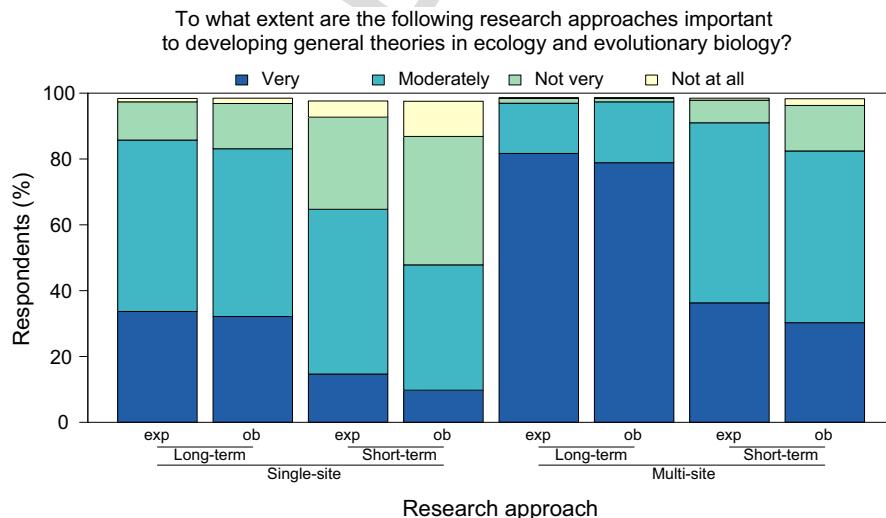


FIG. 3. In an online questionnaire on long-term research, completed by 1,179 respondents, long-term, multi-site, observational (ob) and experimental (ex) research were the most frequently cited research approaches considered “very important” for developing general theories in ecology and evolutionary biology. Four levels of importance were given for selection, ranging from very to not at all important. Bars do not sum to 100% given the small proportion of respondents who entered “not sure” or who did not respond to this question.

1 concurred on the importance of long-term, multi-site
2 observational and experimental approaches (Wilcoxon
3 signed-rank test, $Z = -1.64$, $P = 0.1$; Appendix S1:
4 Table S4), valuing both approaches equally important for
5 developing general theories in ecology and evolutionary
6 biology (Fig. 3). This finding is particularly timely
7 as high-cost, multi-site, observational networks (e.g.,
8 NEON) emerge because what it suggests is that funding
9 decisions need to balance the importance of both long-
10 term observational and experimental approaches. Notably,
11 respondents strongly emphasized the value of long- as
12 opposed to short-term research, with 2.5 times more
13 respondents scoring multi-site, long-term, experimental or
14 observational research “very important” relative to the
15 same approaches conducted in the short-term ($Z = -22.8$
16 and -23.6 respectively, $P < 0.0001$; Appendix S1:
17 Table S4; Fig. 3). Equally, single-site research, whether
18 observational or experimental, or short- vs. long-term,
19 was considered much less important for developing general
20 theory than multi-site, long-term approaches (Fig. 3).
21 These questionnaire responses provide a rationale (i.e.,
22 importance for generating understanding) for supporting
23 the rapidly growing number of bottom-up initiated multi-
24 site, long-term experiments (Adler et al. 2011, Barney
25 et al. 2015) and the value of top-down approaches for
26 strengthening and building existing and new networks
27 (U.S. Long Term Ecological Research Network [LTER]
28 2007, Michaels and Power 2015).

29 Further, the number of respondents who said long-
30 term research at multiple sites was a “very important”
31 approach for developing general theory was 1.7 times
32 higher than for two other approaches, described as “theo-
33 retical models that consider common biological processes
34 rather than a single organism” and “literature/database
35 syntheses of variables from a large number of species or
36 systems”. The least supported approach for developing
37 general theory was the use of “laboratory model organ-
38 isms or systems used to represent common biological
39 processes rather than any one organism or system.” It
40 was rated as “very important” five times less often than
41 multi-site, long-term research (Fig. 3). Overall, multi-site,
42 long-term research, whether observational or experimen-
43 tal, was by far the most highly ranked approach for
44 developing general theory (Fig. 3). Community support
45 for approaches that most advance the development of
46 general theory resoundingly advocate for multi-site, long-
47 term, experimental and observational work.

48 *Topics and questions to address*

49
50
51 Given the overwhelming support for the value of long-
52 term, multi-site research to generate understanding and
53 theory related to ecological and evolutionary science, the
54 topics and questions that respondents identified as being
55 the most important for future long-term research take
56 on particular relevance (Table 1). We asked each respon-
57 dent to list up to three research topics and/or questions
58 that are the most important for future LTREE to

address. In this section (and the next), given that we had
open-ended questions with a defined maximum (i.e.,
three) number of responses per respondent, we provide
count data only and not proportions. From the
responses, we identified 12 primary topics and 18 sec-
ondary topics and representative questions associated
with each (Appendix S1: Table S1).

By far the most commonly identified research topic
was the impact of global change, including climate
change, invasion by nonnative species, and anthropogenic
disturbance, on populations, communities, ecosystems,
and evolutionary processes ($n = 1,352$). Most respon-
dents said that human-induced drivers of global change
were the most important topic for LTREE. Climate
change was the single largest secondary topic area within
“global change,” likely because climatic changes take
place over many years, making LTREE approaches well
suited for assessing their impacts. The selection may also
reflect the sense of urgency around climate change, given
the unprecedented rate of change, global footprint, and
potential to fundamentally alter the environment and
ecology of all ecosystems (Parmesan and Yohe 2003,
IPCC 2014). The impacts of natural disturbances (e.g.,
fire, hurricanes, drought), which may be amplified in fre-
quency and/or duration by climate change (Trenberth
et al. 2013, Cai et al. 2014, Cochrane et al. 2015), were
also commonly listed as a secondary topic area. This is
likely because long-term research is particularly suited to
studying disturbances that may be infrequent and/or that
influence systems long after the disturbance event (Lin-
denmayer et al. 2010, Dodds et al. 2012).

Following climate change, the next four primary topic
areas could be interpreted as levels of organization and/
or disciplinary foci. Most common was “ecosystem,”
which was listed about half as commonly ($n = 749$) as
“global change” and about twice as commonly as “popu-
lation ecology” ($n = 391$). Next came “community ecol-
ogy” ($n = 259$) and then “evolution” ($n = 193$). The
ordering of these topic areas was not a simple reflection
of the areas of expertise listed by the respondents
because, for example, about six times more respondents
listed community rather than population ecology as
their primary expertise (Fig. 1). Likewise, because
ecosystem and population were ranked ahead of com-
munity as important primary topic areas for long-term
research, the ranking also does not simply reflect the
perceived usefulness of long-term approaches for
addressing questions at higher (or lower) organizational
levels and/or on areas that long-term experimental
research is generally perceived to have most advanced
understanding (Fig. 2). It could be that selection of
ecosystem and population ahead of community reflects
the greater ease with which ecosystem (spatial area) and
populations (all individuals of a single species) are oper-
ationally defined, at least within terrestrial systems
(Lawton 1999). Yet what is perhaps most striking is the
commonality across these disciplinary foci in many of
the representative questions, in terms of how frequently

TABLE 1. Research topics and representative questions considered most important for future long-term ecological and evolutionary research.

Research topics	Representative questions
Global change (n = 1,352)	What are the effects of multiple global change drivers on ecosystems, communities, or populations? How are populations evolving and/or adapting to global change drivers?
Climate change	What are population-level adaptive responses to climate change? How does climate change impact the evolution of populations? What are the effects of climate change on ecosystems, communities, and/or populations? What are the effects of ocean acidification?
Natural disturbance	How do changes in environmental disturbances such as fire, floods, or drought affect evolution, ecosystems, communities, and/or populations?
Invasive species	How do ecosystem functions change in response to invasion by nonnative species? Are there unexpected interactions between resident and invasive species? What are the community and ecosystem consequences of these altered interactions? What are the long-term responses of populations, communities and/or ecosystems to invasion by nonnative species?
Disease	How will outbreak dynamics shift in response to changes in disturbance regimes and/or global change drivers?
Other anthropogenic disturbances	What are the long-term effects of (1) pollution (chemical contaminants and macro-debris [plastics]), (2) nitrogen deposition, (3) human population growth, (4) human harvest of natural resources, (5) landscape fragmentation, land use change, and habitat loss, (6) genetically modified organisms, or (7) energy extraction on populations, communities, ecosystems, and/or evolutionary processes?
Ecosystem ecology (n = 749)	How does ecosystem stability change through time? How should we integrate long-term data into Earth system and biogeochemical models? What are ecosystem responses to pulse and press events/perturbations? How do ecosystem processes change across spatial and temporal scales?
Ecosystem restoration	What are the possible trajectories of populations, communities and/or ecosystems to restoration? Are responses to ecological restoration transient or stable?
Biodiversity–ecosystem function	What are the consequences of biodiversity loss on ecosystem functions over long-time scales?
Ecosystem resilience	What factors determine ecosystem resilience to natural and anthropogenic disturbances?
Ecosystem services	How should we measure, manage, and maintain ecosystem services? How do ecosystem services change through time?
Population ecology (n = 391)	What are the long-term demographic consequences of short-term phenomena?
Species distributions	How are dispersal, migration, and distributions of species responding to environmental changes?
Phenology	What potential phenological mismatches will arise as populations respond to global change drivers? How will population phenology respond to global change?
Community ecology (n = 259)	How do co-evolutionary processes influence community composition? What role do rare events have in shaping community structure?
Trophic interactions	What are the impacts of trophic downgrading? How does food web structure influence ecosystem functions? How do trophic interactions respond to global change?
Succession	What are the long-term effects of global change and altered disturbance regimes on successional dynamics?
Species interactions	What are the long-term dynamics of species interactions at range boundaries? How will species interactions respond to the loss and gain of species through time? How will species interactions respond to global change drivers?
Evolution (n = 193)	How are organisms adapting to environmental change? How quickly are organisms evolving or co-evolving in novel environments? How are the rates of evolution distributed relative to rates of environmental change? Does this predict evolution or extinction of populations? What are the relative roles of phenotypic plasticity and genetic adaptation to environmental change?
Evolutionary ecology	Are eco-evolutionary feedbacks predictable over the long-term? What are the eco-evolutionary consequences of species interactions (especially novel interactions with nonnative, invasive species)? How important is acclimation or microevolution in shaping long-term ecological responses?
Coupled human–natural systems (n = 176)	How can we better integrate long-term research into policy decisions? What are the consequences of the loss of natural processes and their replacement by human-managed systems? What are effective measures of ecosystem resiliency for guiding sustainable development?
Agro-ecology	What are the best long-term sustainable agriculture practices in context of global change? How is agricultural expansion and intensification affecting ecosystems, communities, and/or populations? How can we manage agricultural systems for ecosystem multi-functionality and resilience?

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TABLE 1. (Continued)

Research topics	Representative questions
Urban ecology	What are the impacts of urbanization on landscapes, ecosystems, communities, and/or populations?
Sustainable human use of resources	How do contemporary human activities alter the long-term sustainability of ecosystem services?
Freshwater and marine ecology ($n = 84$)	What are the spatial, seasonal, and temporal variations in aquatic (freshwater and marine) biogeochemical cycles? What are the long-term impacts of ocean acidification and warming on marine ecosystems?
Conservation ($n = 65$)	What is the long-term effectiveness of contemporary restoration and conservation activities? What role should habitat refugia, conservation corridors, and species relocation have in protecting species from global change?
Modeling/Ecological theory ($n = 63$)	What are the ecological thresholds or tipping points that lead to alternative stable states or alterations in trajectories? How common are discontinuous transitions and alternative stable states? How can long-term data be used to test ecological theory and models?
Experimental design ($n = 48$)	What is the relationship between short-term and long-term observations? Can we capitalize on “natural experiments” and natural change through time to understand population, community, and/or ecosystem processes? What are the appropriate time scales for data collection on different topics?
Microbial ecology ($n = 27$)	How should we integrate microbial studies into long-term research? How stable are microbial communities?

Notes: Topics and questions were summarized from 1,179 respondents who provided over 3,500 open-ended responses to an online questionnaire on long-term, experimental research in ecology and evolution. Topics were given a primary code and a narrower secondary code (indented). See Appendix S1 for information on thematic coding of responses. Summarized responses are presented from most to least commonly identified primary topic.

the impacts of global change are a motivating force. Global change as a driver is an integrating theme, with those working on evolutionary dynamics and all levels of ecological organization viewing these impacts among the most important questions for LTREE to address.

Further, many representative questions touch on themes that have motivated the fields for many decades (e.g., system stability and resilience) but with foci that represent more recent trends toward ecological management and services (e.g., restoration and ecosystem services). Coupled with the motivation of global change impacts, the questionnaire responses therefore reflect a strong community need to understand how human impacts, management and use shape ecological and evolutionary dynamics. These outcomes appear to parallel recent findings that long-term research is disproportionately represented in conservation policy relative to short-term research (Hughes et al. 2017). A lower but still substantial number of respondents listed “coupled human-natural systems” ($n = 173$) as a primary topic, though in our coding this topic was fairly narrowly defined and restricted to answers about systems historically defined as “managed” or “human-dominated” (e.g., urban or agriculture; Table 1). Even for systems considered “natural” or “pristine,” the abundance of questions related to human-caused environmental change illustrate that scientists view human impacts, decisions, and actions as key forces shaping ecology and evolution, and the important role for LTREE in understanding the consequences.

Three further insights stood out in the coding and interpretation of the topics/questions that respondents said were most important for LTREE to address. The first were the linkages between evolution and long-term

ecological dynamics emphasized in the representative questions for the primary topic area of “evolution” (Table 1). For example, is the rate of adaptation fast enough to allow evolution of a population or will it lead to extinction in a changing environment? How will microevolution shape ecological responses, and what are the eco-evolutionary consequences of species interactions? Such research questions emphasize the need to consider evolutionary dynamics if we are to understand ecological patterns in the longer term. Second, representative questions under the “coupled human–natural systems” code emphasized the need to understand how ecological responses in turn shape human wellbeing and decision making (Table 1). Such foci highlight the growing awareness that human wellbeing is strongly dependent on ecological processes (Levy et al. 2005).

Finally, “microbial ecology” was surprisingly the least commonly cited of the 12 primary topics ($n = 27$). Given the proliferation of technologies to understand microbes from genomic to metabolic levels, the structure and function of microbial communities is a research area currently receiving substantial funding and attention (Stulberg et al. 2016). This lack of emphasis on microbial ecology as a target of LTREE might then reflect a limitation of analyzing open-ended questions. Many responses were short and may not fully reflect the views of respondents. For example, respondents might have been thinking of microbes when they listed questions under numerous other topic areas, given that adaptation, community shifts, and demography all apply equally to microbial and macrobial communities, and microbes also are the engines that drive many ecosystem/biogeochemical processes (Falkowski et al. 2008). However,

representative questions such as, “How do we incorporate microbes into long-term studies?” might also suggest challenges for integration of microbial foci into LTREE. These challenges may arise because of the common perception that microbial communities react rapidly and harbor huge functional redundancy (Martiny et al. 2006, Green et al. 2008, Strickland et al. 2009), making their long-term response less interesting or important. Such perceptions do appear to be changing. For example, emerging efforts to represent microbial processes explicitly in biogeochemical models increasingly reveal that long-term ecosystem consequences might arise from underlying microbial dynamics (Wieder et al. 2013, Bradford et al. 2016), suggesting the need to consider their long-term responses in LTREE initiatives.

Barriers and incentives

We used a combination of closed and open questions to identify barriers and incentives for engaging in LTREE. For the closed question, respondents were offered a range of options and asked to rate them on a scale from “very important” to “not at all important” for encouraging scientists to engage (Fig. 4). For the two open-ended questions, respondents were asked to list up to three primary barriers and three primary incentives to

conducting LTREE. Open-ended responses were coded into five primary and 22 specific categories of barriers, and nine primary and 16 specific categories of incentives (Appendix S1: Tables S2, S3; Fig. 5).

There was significant overlap among barriers and incentives. The most frequently reported barrier to LTREE was research funding ($n = 856$), with the majority of respondents citing its general lack. More specific issues that were particularly challenging for initiating or maintaining long-term research included the length of most research grants (<3 yr) and limited funding sources for new long-term projects or to maintain infrastructure. Further, current funding mechanisms were criticized for being skewed towards new projects in lieu of continued funding for long-term studies, mirroring a recently quantified trend showing decreased funding for long-term research, and increasing funding for short-term studies (Hughes et al. 2017). Consistent with these barriers, closed-ended responses to do with longer-term funding, new project monies, and maintenance of site infrastructure were most commonly ranked as very important for encouraging LTREE (Fig. 4). More positively, funding was the second most-frequent response ($n = 421$) to the open-ended question on incentives for conducting long-term research (Fig. 5). The most often reported ($n = 542$) incentive for conducting LTREE was to gain a

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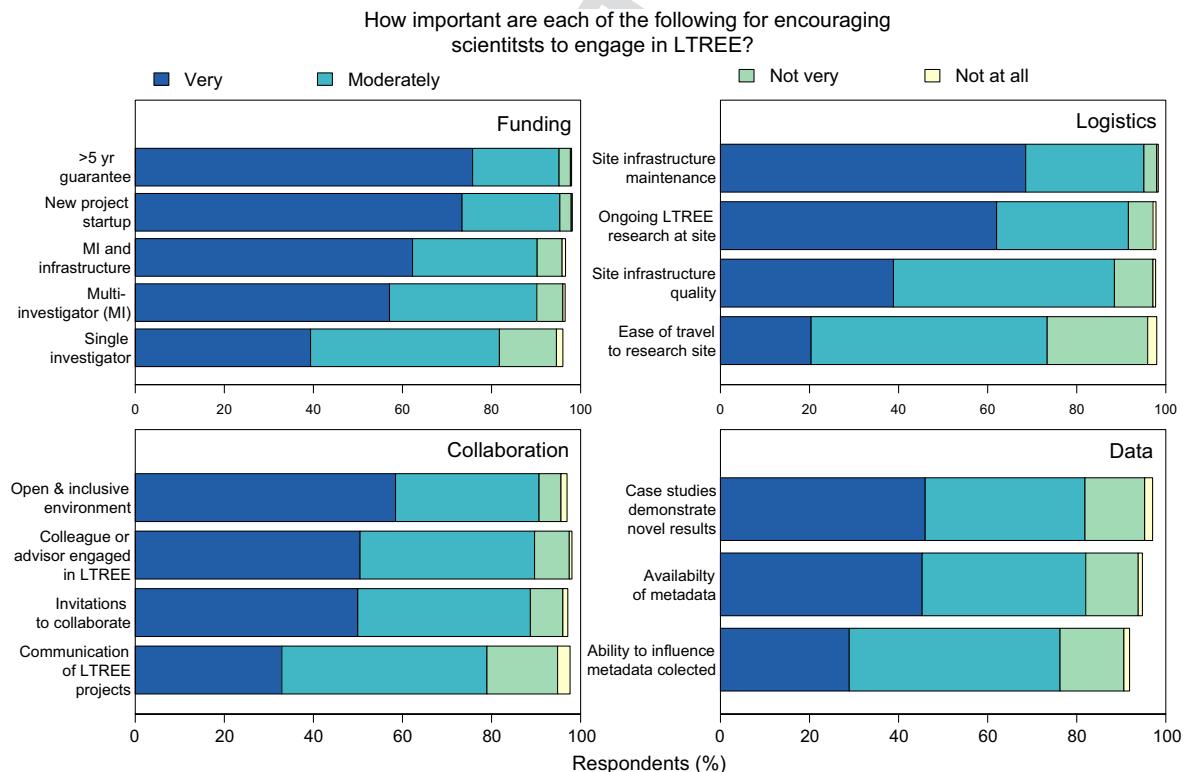


FIG. 4. Respondents ($n = 1,179$) to a questionnaire on long-term research in ecology and evolution (LTREE) were asked to rate the importance of 16 motivators for encouraging participation in LTREE. Four levels of importance were given for selection, ranging from very to not at all important. Bars do not sum to 100% given the small proportion of respondents who entered “not sure” or who did not respond to this question.

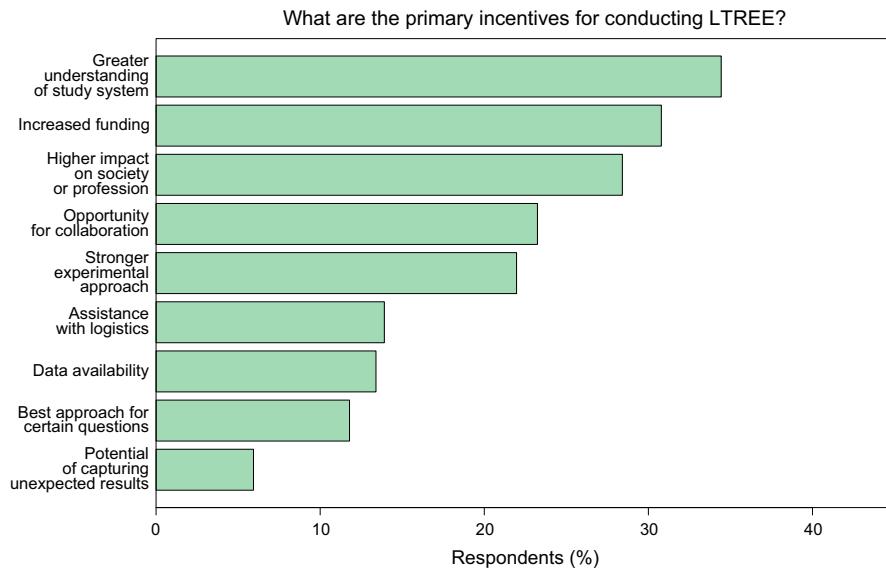


FIG. 5. Primary thematic categories coded from responses to an open-ended question on what respondents felt were the three most important incentives for conducting long-term research in ecology and evolution (LTREE). Top reasons were to gain a greater or deeper understanding of the system of study (understanding), increased research funding (funding), and the potential for greater impact on a researcher's professional career or for addressing important questions (impact). Percentages are based on 2,671 responses from the 971 (of 1,179 total) respondents.

greater understanding of the study system. This finding was consistent with the consensus from the closed-ended question about research approaches, where long-term, multi-site research was identified as most important for generating ecological understanding and for developing general theory (Fig. 3). The trade-off for LTREE then seems to be that funding for long-term work is particularly challenging to obtain and maintain, whereas the perceived pay-off is greatest in terms of developing ecological and evolutionary knowledge (Fig. 5). Notably, a number ($n = 200$) of responses to the incentives question highlighted the advantage that, at least in the United States, long-term research has some dedicated funding programs.

Respondents expressed various motivations for the importance of LTREE for developing system understanding, including gaining a "deeper" or "holistic" understanding ($n = 204$), for developing and refining ecological theory ($n = 71$), or satisfying personal curiosity ($n = 61$). Closely related to the "understanding" category, was the frequent assertion ($n = 332$) that the "experimental approach" is the strongest for capturing particular dimensions of ecological dynamics (Fig. 5). Under this category, for example, respondents noted that LTREE was an appropriate means of studying processes that unfold over long time scales or to study organisms with longer life spans. Equally, they said LTREE provides insights into the importance of transient or cyclical stochasticity that might obfuscate the interpretation of short-term dynamics, and is most likely to capture data during infrequent environmental events. Further, they noted that long-term studies provide a record of historical, baseline data

required for understanding how environmental change is shifting dynamics. Notably, less experienced scientists more strongly ranked the importance of the experimental approach than more experienced scientists, whereas more experienced scientists more strongly ranked the benefit of LTREE for generating understanding (Table 2), despite the fact the two seem intimately related. It is not clear as to what underlies this experience-associated difference of opinion, but similarly strong experience-related differences were apparent also for primary categories scoring data availability, funding, logistics, and impact (Table 2).

TABLE 2. The likelihood of certain types of responses to an open-ended question on the primary incentives for conducting long-term research were significantly influenced by the respondent's years of research experience.

Incentive type	Coefficient	SE	<i>P</i>
Collaboration opportunity	0.062	0.054	0.254
Data availability	-0.250	0.073	0.001
Experimental approach	-0.138	0.057	0.016
Funding availability	0.251	0.050	0.000
Impact	0.191	0.051	0.000
Logistics	0.179	0.065	0.006
Understanding	0.233	0.094	0.013
Unexpected findings	0.062	0.054	0.248

Notes: Coefficients are from a binary logistic regression on the likelihood of reporting a given type of incentive based on the years of experience. Negative coefficient values indicate that earlier-stage researchers were more likely to list an incentive than more experienced researchers and vice-versa. Coefficient size (independent of sign) can be used to compare the relative importance of one incentive type vs. another.

Given that long-term research by necessity relies on the upcoming generation of scientists to continue it, greater exploration of these experience-related differences in motivation may be important for the successful establishment and continuation of LTREE programs.

Over one-quarter of the barriers reported by respondents reflected systemic barriers within and outside of academia that hindered LTREE efforts ($n = 571$). These included the pressure to publish frequently, where there was the perception that LTREE led to a delayed and limited number of peer-reviewed publications, and hence limited support from university administrators. Conversely, a common response category of incentives for LTREE research was the potential impact of that research ($n = 420$). Within this category, responses were evenly split between the potential for positive impact on the researcher's professional career ($n = 170$) and for addressing important problems facing society, including biodiversity loss and global change ($n = 159$). In terms of professional impacts, respondents noted that LTREE had the potential for publication in higher-impact journals, a greater number of publications in the long-term, and more recognition among other researchers. Taken together, these responses are consistent with recent findings that LTREE tends to have higher impact than shorter-term work (Hughes et al. 2017), whereas there are significant impediments for engaging new researchers in LTREE. Given the greater pay-offs personally and for generating ecological and evolutionary understanding, we suggest that there is a need to develop mechanisms (e.g., prestigious fellowships) that help overcome these impediments.

Other commonly reported barrier categories included "logistic" ($n = 441$), with lack of infrastructure and its maintenance most frequently reported, as well as issues related to recruiting, training, and managing personnel. These personnel issues typically were characterized as time-consuming, with personnel turnover creating difficulties with maintaining continuity in data collection and maintenance of experiments. Far fewer respondents listed access to research sites ($n = 155$) or data availability ($n = 115$) as barriers, which matched with the lower relative importance of variables such as ease of travel and data access, in the closed-ended question about mechanisms to engage researchers in LTREE (Fig. 4). The lower barriers associated with access and data perhaps emerge from the increasing emphasis on collaborative networks and open-access data archiving. Notably, approximately one-half of the correspondents rated an open and inclusive research environment as very important for engaging researchers in LTREE (Fig. 4). Respondents also frequently cited ($n = 300$) opportunities for engaging in new and interdisciplinary collaborations to address big, complex issues as a primary incentive for LTREE (Fig. 5). Collectively, these closed- and open-ended responses appear to emphasize the importance of developing professional skills, such as teamwork, interpersonal communication, positivity, and negotiation, to create a working

environment best situated to resolve the complexities of long-term ecological and evolutionary dynamics.

CONCLUSIONS

The Long-Term Ecological and Evolutionary Research Survey (Bradford et al. 2017) was designed to explore the views of scientists in the ecology and evolutionary biology fields on long-term research. Some of the survey findings corroborate views captured in other published reports on the benefits and failings of LTREE activities (Ducklow et al. 2009, Clutton-Brock and Sheldon 2010, Lindenmayer et al. 2010, Magurran 2010, Michaels and Power 2015, Hughes et al. 2017). However, our survey complements prior assessments by providing community-wide perspectives on LTREE regarding its role in developing theory and understanding, the most important topics and questions for it to address, and the primary barriers and incentives for engagement. Surveys also provide an inclusive mechanism, when repeated, to track perspectives on whether new initiatives have helped to advance research priorities. Like any assessment, there are limitations to our approach. For example, thematic coding of open-ended responses might misinterpret the intended point of a response. Further, the survey was primarily targeted at those working for U.S. institutions, and so it is unknown as to whether the views expressed are representative of the global research community. Nevertheless, the responses provide valuable insights for setting the strategic direction of LTREE activities.

Specifically, long-term, multi-site research was rated the most highly valued approach for generating understanding and for developing general theory. Both observational and experimental approaches were considered equally important, and well positioned to investigate the most pressing environmental challenges arising from human-induced global change. The potential contributions of incorporating evolutionary science into long-term research were apparent, for building understanding across all levels of ecological organization. Short-term funding and fewer publications were particularly acute career barriers for beginning scientists to engage in LTREE, but the longer-term impact of engaging on both an individual's career and for advancing knowledge were widely perceived. Creating a research environment and funding structure that promotes long-term observational and experimental research therefore appears to require short-term changes that promise long-term payoffs for understanding ecological and evolutionary dynamics.

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