

OPINION ARTICLE

# Eco-evolutionary dynamics in restored communities and ecosystems

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Recent ecological studies have revealed that rapid evolution within populations can have significant impacts on the ecological dynamics of communities and ecosystems. These eco-evolutionary dynamics (EED) are likely to have substantial and quantifiable effects in restored habitats over timescales that are relevant for the conservation and restoration of small populations and threatened communities. Restored habitats may serve as “hotspots” for EED due to mismatches between transplanted genotypes and the restored environment, and novel interactions among lineages that do not share a coevolutionary history, both of which can generate strong selection for rapid evolutionary change that has immediate demographic consequences. Rapid evolution that influences population dynamics and community processes is likely to have particularly large effects during the establishment phase of restoration efforts. Finally, restoration activities and their associated long-term monitoring programs provide outstanding opportunities for using eco-evolutionary experimental approaches. Results from such studies will address questions about the effects of rapid evolutionary change on the ecological dynamics of populations and interacting species, while simultaneously providing critical, but currently overlooked, information for conservation practices.

**Key words:** conservation genetics, evolutionary potential, rapid evolution, reintroduction, restoration genetics, translocation

## Implications for Practice

- The success of restorations can be improved by understanding how feedbacks between ecological dynamics and rapid evolutionary change of translocated populations unfold in the restored environment, and the effects of these interactions on the establishment, development, and persistence of restored ecological communities.
- Practitioners and scientists should integrate long-term ecological monitoring data with measurements of phenotypic traits over time to quantify eco-evolutionary dynamics in restored communities.
- Results from these studies will provide practitioners with improved guidelines for how to choose genetic sources of propagules to increase the success of restored populations and communities.

## Introduction

Ecological restoration is an increasingly important solution for repairing damaged ecosystems and creating suitable habitat for species threatened by habitat loss, degradation, and fragmentation (SERI 2004). When feasible, strategies for habitat restoration involve careful consideration of the geographic and ecological origins of propagules (e.g. seeds or transplants), as local adaptation and the amount of genetic variation are expected to be important determinants of restoration success (Montalvo et al. 1997; Lesica & Allendorf 1999; Hufford & Mazer 2003; Rice & Emery 2003; Mijangos et al. 2015). However, the specific links between the initial genetic structure and the evolutionary change caused by selection in response to

translocation still remains largely unexplored in restoration contexts. In particular, few studies have directly measured the influence of rapid evolution on populations that are introduced into restored environments (but see Kulpa & Leger 2013). Recently, ecologists have developed novel approaches that make it possible to measure feedbacks between rapid evolutionary change and population dynamics, or “eco-evolutionary dynamics” (hereafter referred to as EED). The origins of EED can be traced back to Pimentel (1961), whose model predicted oscillations in herbivore population densities when host plant genotypes varied in their degree of herbivore resistance. Since then, numerous studies have explored how EED operate in natural systems using various experimental approaches (e.g. Abram 2000; Whitham et al. 2003; Johnson & Stinchcombe 2007). Results from these and other EED studies have demonstrated that evolutionary change can occur over timescales as short as a single generation, and that these changes can influence the ecological dynamics of populations, communities, and ecosystems (Pelletier et al. 2009; Schoener 2011). These changes in turn shape patterns of selection in subsequent generations (Hairston et al. 2005; Palkovacs & Hendry 2010; Schoener 2011). Collectively, the

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results of these and other studies in natural systems suggest that rapid evolutionary change may play an important role in the success and persistence of restored populations and communities.

Recent studies from natural systems indicate that selective pressures can be strong when there is a mismatch between genotypes and the abiotic and biotic conditions of the restoration site (Palkovacs et al. 2008; Bassar et al. 2012; Kulpa & Leger 2013). A mismatch may occur when economic or logistical constraints preclude the use of local source populations, in habitats that have become so degraded or altered that no putatively locally adapted population exists for that site, or when there is insufficient planning to match propagule sources to the environmental conditions at the recipient site (Kettenring et al. 2014). To reduce mismatches between genotypes and the restored environment, managers may prioritize the selection source of populations by selecting geographically proximate or ecologically similar populations, under the assumption that those lineages will be better adapted to the conditions at the restoration site (McKay et al. 2005; Breed et al. 2013). Alternatively, managers may choose to create a mix of genotypes collected from different source populations to maximize genetic diversity in the founding population, with the long-term goal of maximizing the ability to adapt to future environmental change (Lesica & Allendorf 1999; Broadhurst et al. 2008; Kettenring et al. 2014). Despite these efforts, it is unlikely that restored environments will ever perfectly match the conditions experienced by populations in their home environment (Breed et al. 2013), and will instead generate strong selective pressures for rapid evolution in the introduced populations.

Here, we argue that restorations provide ecological arenas in which EED are likely to be particularly strong (see Box 1 for a hypothetical example of EED in a restoration). Anthropogenic manipulations involved in creating or improving habitat can generate patterns of selection that contrast sharply with those that characterize the recent evolutionary history of the translocated populations. We suggest that the study of EED in restored communities and ecosystems will provide important insights into the role of genetic processes shaping the establishment and long-term success of ecological restoration efforts. Importantly, restoration managers often have access to information about the genetic composition and the home environment of the initial “donor populations” prior to their introduction, providing an experimental control that is often lacking in studies that are conducted in unmanaged systems. This information makes it feasible for managers to monitor EED in restored communities and quantify the extent to which these dynamics influence establishment and the long-term success of restoration efforts. Finally, we offer suggestions for how recently developed methods for quantifying EED can be integrated into existing restoration protocols.

## Causes of EED in Restoration Settings

### Restorations as Hotspots for Rapid Evolution

The mismatch between the environment of a restored or created habitat and the conditions to which source populations

were previously adapted can generate strong selection for rapid evolutionary change in the newly introduced populations (Rice & Emery 2003; Agrawal et al. 2012). At first, strong selection may reduce population size, growth rate, and mean fitness, especially if there are low initial levels of genetic variation due to inbreeding or population bottlenecks (Shaw et al. 2015). However, if there is genetic variation for adaptive traits in the population, this initial reduction in fitness could be followed by a rapid evolutionary response and eventually adaptation to the new environment (Montalvo et al. 1997). It is necessary to consider both the genetic composition of a population and the selective pressures in the restoration environment to predict the persistence of populations in restorations (Falconer & Mackay 1996), because both influence whether adaptive evolution can occur in a population. To our knowledge, only one study has directly measured evolutionary change in a population that has been introduced into a restored habitat (Table 1, A; Kulpa & Leger 2013), and no studies have investigated the effects of evolutionary change in restored populations on intraspecific and interspecific ecological dynamics.

Examples from studies in manipulated, natural populations provide evidence that populations of interacting species that do not share a recent coevolutionary history may impose strong selective pressures on one another (Table 1, A; Fussmann et al. 2007; Palkovacs et al. 2009; Crutsinger 2016). This suggests that introducing community members from different sources into a common restoration site could generate EED during the initial stages of community assembly and establishment. For example, choosing to use plant ecotypes that do not have a coevolutionary history with the local arbuscular mycorrhizae fungi in a prairie restoration may cause strong selective pressures on both species, which would in turn influence the population size and growth rates (Johnson et al. 2010).

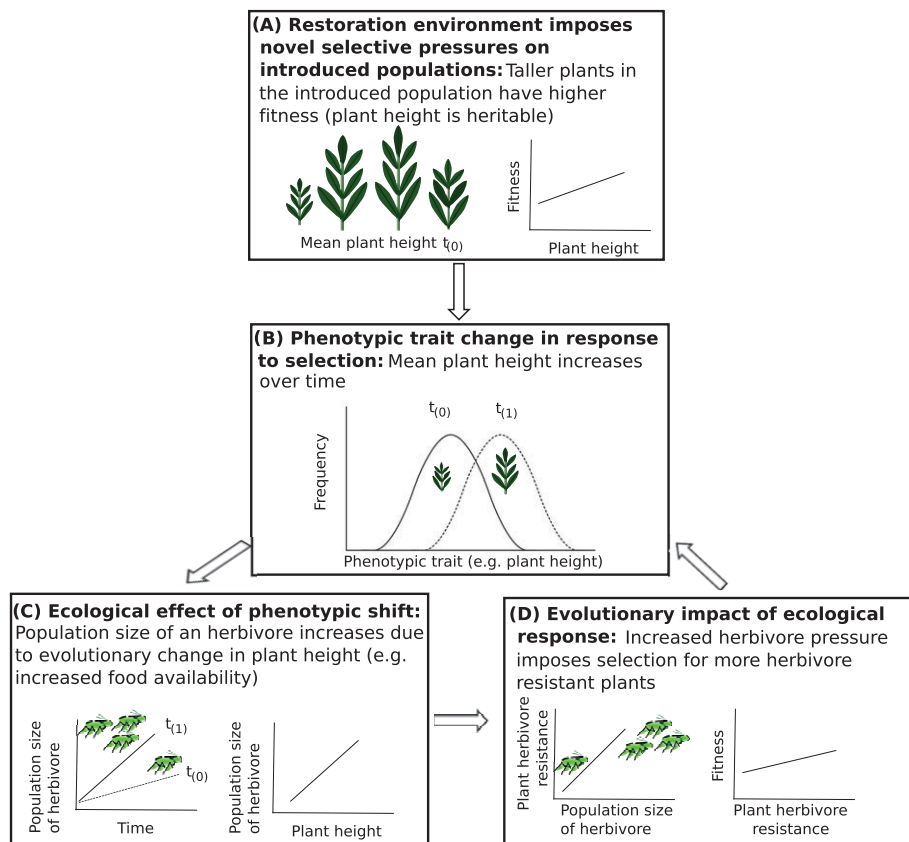
### Consequences of Rapid Evolution for Restored Communities and Ecosystems

In a restoration setting, novel interactions among species can be a strong source of natural selection with consequences that can reverberate throughout the community (Table 1, B). Indeed, species interactions have been shown to be one of the most common mechanisms generating EED (Koch et al. 2014). Hiltunen and Becks (2014) developed an EED model of predator–prey dynamics and found that when compared to a purely ecological model that did not allow for prey evolution, the EED model could better explain the cycling of predator–prey population patterns in 19 out of 21 previous studies. Rapid evolution that influences community processes, such as predator–prey, plant–herbivore, and interspecific competitive interactions, can also influence the establishment and long-term success of restoration activities (Table 1, B; Whitham et al. 2003).

Dominant and keystone species are expected to have a disproportionately large influence on community assembly during the early establishment phases of restorations (Gibson et al. 2012; Baer et al. 2014). Consequently, rapid evolution in dominant and keystone species is likely to have particularly large effects on community dynamics (Table 1, B; Johnson & Stinchcombe 2007). For example, dam construction caused evolution in a

### Box 1. Hypothetical example of EED in habitat restorations.

Eco-evolutionary dynamics may occur in restored environments when the introduced genotypes encounter new patterns of selection than those that characterized their home environment. If there is genetic variation in the introduced populations for traits that influence fitness in the restored environment, novel selective pressures can promote rapid evolutionary change (i.e. over one to a few generations), which, in turn, influence population growth trajectories, community dynamics, and ecosystem processes (Palkovacs & Hendry 2010). A hypothetical example of EED operating in the context of habitat restoration is shown here. Propagules of a plant species that experienced different environmental conditions in their homesite are introduced to a newly restored habitat (A). The restored environment favors taller plants, because soil fertility is higher than the homesite and competition among conspecifics for light favors tall plants that can shade out shorter plants. Height is highly heritable, so the mean height of plants in the subsequent generation will increase (B). This increase in height will, in turn, lead to an increase in the population size of a local herbivore that feeds on the plants in response to the increased availability of habitat and food (C). Thus, the rapid evolutionary change in the plant population—which is a response to selection in the restored environment—has a direct effect on the population dynamics of the herbivore. Furthermore, the larger herbivore population generates selection for plants that are more resistant to herbivory, because more resistant plants have greater fitness under increased levels of herbivory than vulnerable plants (D).



keystone fish predator, the alewife (*Alosa pseudoharengus*), that then triggered a trophic cascade in freshwater lakes (Table 1; Palkovacs et al. 2008; Walsh et al. 2012). Knowledge of the amount of genetic diversity in dominant and keystone species, and the evolutionary change that occurs in these species during community establishment, could help managers achieve the desired restored community composition by allowing them to strategically choose source populations with genetic variation that may facilitate adaptation in restoration contexts (Gibson et al. 2012).

### Integrating EED Approaches Into Restoration Practice

Restoration ecology may provide a particularly relevant and tractable context for examining the role of EED in shaping the short- and long-term success of habitat restoration. In many restorations, the genetic composition of founding populations and the initial ecological conditions of the site are documented prior to the introduction of populations (Block et al. 2001). Additionally, restored habitats are often monitored for multiple generations in accordance with management plans.

**Table 1.** Selected examples of eco-evolutionary dynamics from natural systems relevant for restoration ecology.

Example	Study System	Rapid Evolution	Ecological Impact of Rapid Evolution	Example of Potential Influence of Rapid Evolution on Restoration Ecology
<b>(A) Rapid evolution that occurred due to a genetic by environment mismatch</b>				
Mismatch between environment and propagule source	<i>Elymus elymoides</i> ssp. <i>californicus</i> (Kulpa & Leger 2013)	Restoration site selected for smaller plant size, smaller seed size, and earlier flowering time	Hypothesized greater drought tolerance (not yet tested)	Population demographics (e.g. population size and growth rate)
Mismatch in coevolutionary history	<i>Poecilia reticulata</i> , <i>Rivulus hartii</i> (Bassar et al. 2012)	Noncoevolved genotypes of predator select for r-selected life history	Trophic cascade	Local adaptation between different ecotypes (Johnson et al. 2010)
<b>(B) Consequences of rapid evolution for restored communities and ecosystems</b>				
Predator–prey	<i>Chlamydomonas reinhardtii</i> , <i>Brachionus calyciflorus</i> (Becks et al. 2010, 2012; Fischer et al. 2014)	Prey resistance to predator	Influences prey and predator population sizes	Predation and community dynamics
Plant–herbivore	<i>Myzus persicae</i> , <i>Hirschfeldia incana</i> (Turcotte et al. 2011, 2013)	Selection for higher herbivore growth rate	Higher herbivore density on host	Herbivory and community dynamics
Competition	<i>Oenothera biennis</i> , <i>Mompha brevitetella</i> (Agrawal et al. 2012)	Greater competitive ability in <i>O. biennis</i>	Suppresses growth of other plants	Competition and community diversity
Dominant and keystone species	<i>A. pseudoharengus</i> , zooplankton (Palkovacs et al. 2008; Walsh et al. 2012)	Selection for smaller mouth and gill raker spacing in <i>A. pseudoharengus</i> (eat smaller zooplankton)	Reduced body size in zooplankton, reduced zooplankton predation on phytoplankton, and higher net primary productivity	Dominant/keystone species and prairie community assembly (Gibson et al. 2012)



Indeed, restoration ecology has a history of providing experimental opportunities for testing ecological theories, including community assembly, succession, state-transition models, and diversity–function relationships (Young et al. 2005). Increased collaborations between restoration practitioners and research scientists interested in EED would provide outstanding opportunities for intensive long-term studies to solve restoration challenges while providing fundamental insights into the nature of EED during community assembly and establishment.

In unmanaged systems, two complementary approaches have been used to test if EED are occurring: (1) measurement of the long-term effects of evolution on ecology (the “retrospective” approach) or (2) measurement of evolutionary and ecological change as they occur (the “real-time” approach) (Fussmann et al. 2007). The retrospective approach tests for EED by comparing the ecological dynamics of a population that has experienced a specific selective pressure to one that has not been exposed to that pressure (Haloin & Strauss 2008). For example, Hairston et al. (2005) found that evolution in diapause phenology of a freshwater copepod (*Onychodaptomus sanguineus*) helped prevent population extinction by comparing the fitness of evolved individuals to individuals that were resurrected from dormant eggs. The alternative approach to studying EED—the real-time approach—simultaneously measures evolutionary change (either phenotypic traits known to be heritable or genotypic variation) and ecological dynamics as they unfold (Fussmann et al. 2007). Here, the phenotype and ecological parameters are characterized prior to the experimentally induced evolutionary change and at multiple time points thereafter. This approach allows researchers to monitor evolutionary change as it unfolds through time, and to directly monitor the corresponding ecological changes that occur.

Retrospective and real-time approaches both provide sufficient tests for EED, but each methodology has its own strengths and limitations that largely depend on the study goals. A retrospective approach is quicker to implement, because it involves a single comparison between a population that is hypothesized to have undergone rapid evolutionary change that influences ecological dynamics and a nonevolving control. This experiment can be conducted in a common garden environment, which could be an existing restoration site, and the nonevolving control may be leftover seeds from the collection that was used to establish the populations (see below). However, the retrospective approach only reveals post hoc ecological consequences of evolutionary change. Thus, information about the rate of evolutionary change must be inferred using molecular tools or through prior knowledge of when selection initially began (e.g. when a restoration is implemented). In contrast, the real-time approach allows for the direct measurement of the feedbacks between rapid evolution and corresponding population and community dynamics as they occur within an experimental population. The primary drawback to the real-time approach is that it requires multiple generations of data collection, and the starting genetic and ecological conditions must be known. It can also be difficult to partition the effects of ecological and evolutionary change on population and community dynamics because these two processes operate

simultaneously (Fitzpatrick et al. 2015). Similarly, the environmental and genetic influences on heritable phenotypes are also intertwined, and can only be teased apart using genetically structured experimental designs. However, restorations offer experimental opportunities that may overcome the inherent limitations or challenges associated with each approach, and are discussed in detail below.

### Nonevolving Controls in Restorations for the Retrospective Experimental Approach

A properly designed EED experiment, regardless of the approach (retrospective or real-time), requires a control in which ecological dynamics operate without any concurrent evolutionary change (Fussmann et al. 2007). Without a nonevolving control, investigators cannot compare ecological dynamics with versus without evolution, thus preventing definitive conclusions about the role of rapid evolution on the observed ecological dynamics. Nonevolving controls are often relatively easy to obtain in the context of restoration practices by simply saving the seeds of the plant populations that are initially installed into a restored habitat (see Kulpa & Leger 2013 for an example). These “ancestral” seeds can be preserved through proper seed storage practices, and compared to subsequent generations in common gardens (ideally at the restoration site) to test for evolved differences (Franks et al. 2008) and evaluate their effects on the ecological dynamics of the community (e.g. herbivory, interspecific competition, species richness, and diversity). Furthermore, ancestral seeds saved from the initiation of a restoration have experienced the same ecological and evolutionary history as the contemporary seeds prior to the restoration treatment, which is unlikely to be true when using a population from a natural site as the nonevolving control. However, it is important that the propagules saved from different time points are grown through at least two generations in a common garden *before* phenotypic traits are compared to reduce environmentally induced differences in the initial populations (Franks et al. 2008); ideally, even more than two generations would precede these comparisons to maximize the removal of maternal environmental (Hendry 2016) and epigenetic effects (Bossdorf et al. 2010). Researchers must also take precautions to prevent the erosion of genetic differences among populations in the common garden. It is important that the ancestral and contemporary populations remain genetically isolated from one another and other nearby populations, which requires controlled mating events in outcrossing organisms. Additionally, evolution due to selection in the common garden environment must be minimized. This can be done by randomly mating parents within each population type and selecting equal numbers of offspring from each parent (Williams & Hoffman 2009). While these controls take some additional time and attention, the common garden approach can be implemented without much additional expense to test for EED in a variety of taxa, including many plants, microbes (by preserving soil), and some insects (Fig. 1A; see also resurrection ecology; Hairston et al. 2005; Franks et al. 2008).

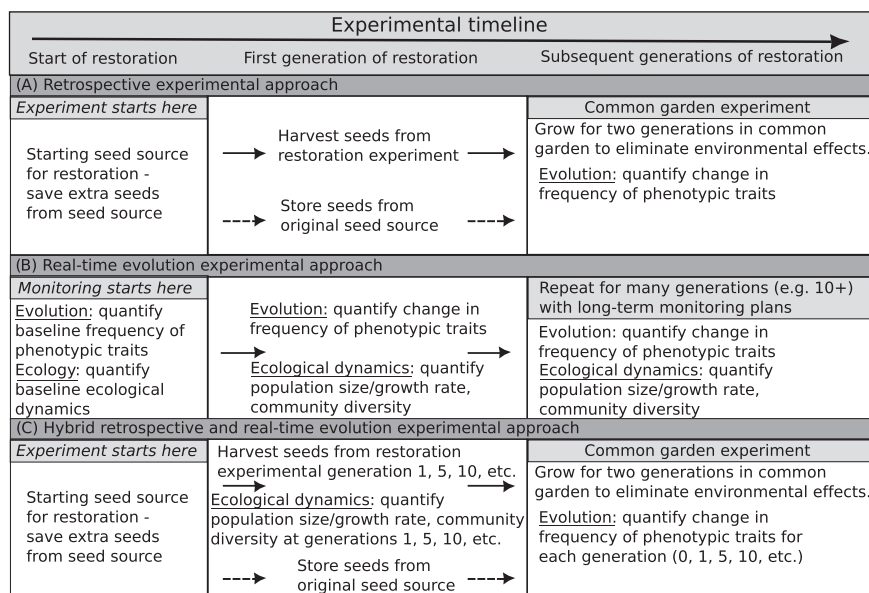


Figure 1. Examples of the retrospective, real-time, and hybrid experimental approaches for measuring EED in restored environments. (A) For the retrospective approach, a nonevolving control that is specific to the restored populations being studied is established by saving a random subsample of the propagules that are used to initiate the restored community. Later, these propagules are grown in a common garden with propagules collected from subsequent generations in the restoration to examine the change in phenotypic traits and ecological dynamics over time. (B) In the real-time approach, phenotypic traits, population, community, and ecosystem dynamics can be measured at the beginning of a restoration and as part of long-term monitoring plans, providing snap shots of evolutionary and ecological change over time. (C) In the hybrid approach, propagules are collected and stored at multiple time points following the population's introduction to a restoration site (generations 1, 5, 10, and so on), and then are eventually grown in a common garden to compare phenotypic traits among representatives of different generations. Ecosystem dynamics are measured during the propagule collection. Solid arrows indicate populations undergoing evolutionary change and dashed arrows represent stored propagules that did not evolve.

### Long-term Monitoring of EED in Restorations With the real time Experimental Approach

It is important to study EED in real time over multiple generations (ideally 10 or more) to determine if rapid evolution causes long-lasting ecological change or only operates in the first few generations of community assembly (Schoener 2011; Shefferson & Salguero-Gomez 2015). However, studies of EED in natural communities have rarely adopted the real-time approach, probably because of the expense of maintaining long-term studies (Fussmann et al. 2007; Schoener 2011) and the challenge of establishing a nonevolving control (Reznick 2013). Restorations provide an outstanding opportunity to combine long-term ecological monitoring data, which is often collected over multiple generations, with measurements of phenotypic traits taken at different time points, starting with the initiation of a restoration (Fig. 1B). Ecological changes that occur over time in restorations are often measured through demographic and community surveys that are included in long-term monitoring plans (Block et al. 2001). Thus, modifying long-term monitoring plans to also include measurements of phenotypic traits that are expected to have a heritable basis could easily allow EED to be quantified in these restoration settings with relatively little additional time and effort (Fig. 1B). Adjustments could be made to the real-time approach depending on the study goal and available resources. For example, EED is likely to be stronger in genetically diverse versus depauperate populations and restoration practitioners interested in comparing the difference in the

strength of EED on restoration success without directly measuring EED with a nonevolving control could record genotype frequencies and restoration success in plots of local genotypes versus a mix of local/nonlocal genotypes.

Even if a trait is known to be heritable, phenotypic plasticity (Hendry 2016) may partially account for phenotypic trait changes over time, especially if the restoration environment itself changes with community establishment. A hybrid of the retrospective and real-time experimental approach could allow for the measurement of differences among traits due to genetics and phenotypic plasticity and corresponding ecological dynamics at different time points in a restoration (Fig. 1C). Propagules could be collected from a restoration at initiation and at subsequent generations over a longer time span (e.g. generations 0, 1, 5, 10, and so on), while ecological dynamics are measured at the same time points as part of a long-term monitoring plan. Propagules from each generation can then be grown in a common garden to test for genetically based differences in phenotypic traits across generations.

### Conclusions

Restorations provide a likely context in which populations lacking a coevolutionary history may experience strong selection for rapid evolutionary change that can influence short-term ecological dynamics. Thus, restoration scenarios provide outstanding opportunities to conduct needed experimental studies

that elucidate how EED shape community assembly processes, while simultaneously providing information that can be useful for the management and conservation of restored communities. Increased collaborations between research practitioners and research scientists would increase and diversify funding opportunities for more long-term studies and more intensive monitoring, while providing access to data from large-scale, long-term projects.

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