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The Resurrection Initiative: Storing Ancestral Genotypes to Capture Evolution in Action

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In rare circumstances, scientists have been able to revive dormant propagules from ancestral populations and rear them with their descendants to make inferences about evolutionary responses to environmental change. Although this is a powerful approach to directly assess microevolution, it has previously depended entirely upon fortuitous conditions to preserve ancestral material. We propose a coordinated effort to collect, preserve, and archive genetic materials today for future studies of evolutionary change—a "resurrection paradigm." The availability of ancestral material that is systematically collected and intentionally stored using best practices will greatly expand our ability to illuminate microevolutionary patterns and processes and to predict ongoing responses of species to global change. In the workshop "Project Baseline," evolutionary biologists and seed storage experts met to discuss establishing a coordinated effort to implement the resurrection paradigm.

Keywords: climate change, microevolution, Project Baseline, resurrection ecology, seed banks

Imagine that naturalists of past centuries had systematically collected and stored representative samples of seeds from the many plant species they encountered in their travels. If this treasure of ancestral material were available to modern scientists, there would be enormous potential to improve our understanding of how the genetic composition of natural populations changes over space and time. By rearing samples of ancestral populations, we could resurrect actual genotypes that existed centuries ago. Differences between modern and ancestral populations would directly document evolutionary change over known time intervals. In this article, we call for an organized effort to accomplish what earlier naturalists did not: systematic collection and preservation of current genetic diversity for future analyses of evolution of phenotypes in conjunction with environmental change. We call this approach the "resurrection paradigm."

The resurrection paradigm

Under the resurrection paradigm, ancestral and descendant genotypes sampled from the same location are grown together in a common environment (Davis et al. 2005). Ancestral genotypes may be obtained from propagules stored either in the research laboratory (artificial seed banks) or in nature (natural seed banks). This approach allows direct and definitive assessment of evolutionary change in phenotypes. If unbiased samples of ancestors and descendants are raised side-by-side, phenotypic differences between the generations can be attributed to microevolutionary change.

Although there are many existing seed banks and germ plasm reserves, often with extensive collections, the resurrection approach for the study of evolution entails new collections for several reasons. First, most current seed banks exist primarily for the purpose of conservation, and thus would be compromised if their stocks were depleted for basic research. Second, even when seed banks contain large collections from a particular species, the samples have often been drawn from just a few locations and thus are of limited utility for studies of spatial genetic variation, including phylogeography. Third, existing seed banks tend not to store multiple offspring from maternal individuals separately. Use of such family structure in the collection strategy would promote application of quantitative genetics in combination with the resurrection approach.

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In a few rare circumstances, investigators have collected dormant propagules from natural strata of different ages and resurrected them for comparison with contemporary populations (Angeler 2007). McGraw and colleagues (1991) grew plants from seeds of graminoids drawn from soil cores at different depths in arctic tundra; seeds from deeper strata represent older populations. When ancestors and descendants were grown in a common environment, plants from seeds buried in deeper soil layers produced fewer leaves than did those from seeds from shallower strata, and plants from different layers also differed in their response to variations in temperature and nutrients (Bennington et al. 1991, Vavrek et al. 1991).

Noting the value of these studies, we raise two concerns about evolutionary studies based on propagules collected from natural seed banks. First, the samples of the gene pool at each time point may be a biased representation of the corresponding population. Seeds that fall to the ground either germinate, die, or enter the seed bank, and these three groups may differ in genetic composition (Tonsor et al. 1993). Second, sediment mixing can occur, and it is not always possible to determine absolute or even relative ages of propagules from sediment layers (Hairston and Kearns 2002).

Intentional storage of ancestral genotypes under controlled laboratory conditions allows the preservation of a less-biased sample of a gene pool of precisely known age (Bennett and Lenski 1999). Applying this approach, Cooper and colleagues (2001) raised replicate lines of *Escherichia coli* in a range of thermal environments and stored frozen samples at several time points across 20,000 generations to capture microevolutionary changes in response to the treatments. When the ancestors and descendants were raised in a common environment, significant differences that were observed among the generations firmly documented evolutionary divergence in growth rates under different temperature regimes. Our vision is to conduct similar temporal collections across a spatial grid in wild plant populations to capture natural selection as it occurs.

The first study to resurrect stored plant material to study microevolutionary responses to climate change in a natural population of annual plants was done by Franks and colleagues (2007). The authors collected seeds of *Brassica rapa* before and after a recent five-year drought in California, and, after a "refresher generation" to minimize maternal effects, raised the ancestors and descendants together in their native habitat (figure 1). The descendants flowered significantly earlier than their ancestors, a finding that the authors interpreted as consistent with life-history theory predicting evolution of early flowering as an adaptation to seasonal drought conditions.

We propose an initiative of systematic seed collections that would allow more rigorous and extensive application of the resurrection approach. Specifically, we are advocating an organized and coordinated scientific research effort to collect seeds from spatial arrays of populations at several time points for each of many plant species. With this material in hand, future evolutionary biologists can revive propagules from the past and examine evolutionary change.

Climate change and an evolution explosion?

The resurrection approach may be especially pertinent given current global climate change, which is occurring at rates and scales not seen for millennia (IPCC 2007). The biological effects of global climate change are already evident in the shifting geographic ranges and phenology (timing of life-history events) of many species (Parmesan 2006). Poleward shifts in species' ranges (such as those following the Pleistocene) may continue, but the rate of shift for favorable climate envelopes may exceed the dispersal capacity of many species (Davis and Shaw 2001). Clearly, ecological changes can dramatically alter selection in local populations. At what rates will populations evolve in response to these pressures,

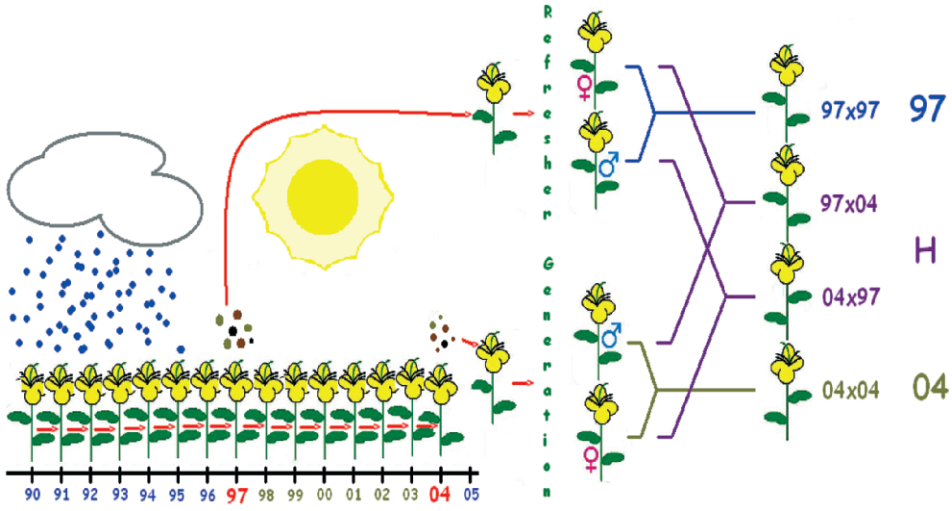

Figure 1. Illustration of the resurrection technique, used here by Franks and colleagues (2007) to study evolution in response to natural drought in* Brassica rapa*. Seeds of* B. rapa *were collected in 1997 after several wet years and again from the same populations in 2004 after a series of dry years. The seeds were then grown in the greenhouse for one "refresher" generation to reduce maternal effects and possible differences in seed quality due to storage. Seeds from these plants were then grown and crossed within the 1997 and 2004 lines, as well as between lines to create hybrids. The resulting offspring were then used in experiments. Differences between 1997 and 2004 lines when the plants were grown under common conditions can be attributed to evolutionary change. Figure courtesy of Sheina Sim, University of Notre Dame.

and will adaptive change make important contributions to species persistence?

There is increasing evidence for genetic shifts in animal and plant populations as a consequence of recent, rapid climate change (Bradshaw and Holzapfel 2008). Reported examples come from studies of fruit flies (Umina et al. 2005, Balanyá et al. 2006), butterflies (Thomas et al. 2001), and pitcher plant mosquitoes (Bradshaw and Holzapfel 2001). These studies used a variety of techniques, including genetic markers, behavioral experiments, analysis of time series of phenotypic data, and pedigree analysis. Each of these approaches has advantages and limitations, and the resurrection paradigm can greatly complement such work.

Project Baseline

The resurrection approach can help to test a wide variety of ecological and evolutionary predictions about how species evolve in response to environmental change (box 1). At a recent workshop titled "Project Baseline," evolutionary biologists and seed storage experts met to plan a concerted effort to collect and store seeds to enable current and future scientists to implement the resurrection paradigm on a broad taxonomic and geographic scale. The workshop, sponsored by the National Science Foundation, was held 9–11 March 2007, at the National Academies' Beckman Center on the campus of the University of California–Irvine. Participants discussed the kinds of questions that can be addressed with the resurrection approach, research opportunities and priorities, and the logistics of implementing a resurrection protocol.

One topic of discussion concerned the kinds of plants that might be included in the initial collections. Annual herbs are appealing candidates, in part because they have short generation times and a potential for rapid evolutionary change, they may offer early warning of negative environmental impacts, and in some cases they are being developed as model genetic systems. At the other end of the life-history spectrum, it would be important to include some long-lived species because they predominate in many communities, provide important economic benefits (e.g., timber crops), and can be used to address issues of ecological sustainability. Discussions also addressed collection and storage protocols, as well as possible experimental designs in the eventual intergeneration comparisons.

Combining techniques for deeper evolutionary insights. The resurrection paradigm makes it possible to design experiments that directly compare the phenotypes expressed by ancestral with descendant populations growing in common conditions, including natural environments. Such experiments will reveal the magnitude of change in traits over the intervening decades. More important, these collections can be used to elucidate the genetic basis of evolutionary change in natural populations in unprecedented detail. Formal genetic crosses among plants representing the ancestral populations would permit estimation of quantitative genetic parameters (i.e., genetic variance-covariance matrices) as a basis for inferring the selection that accounts for changes in mean phenotype between ancestral and descendant populations. Ever-advancing genomic and bioinformatic approaches will reveal concomitant changes at the molecular level.

Box 1. Predictions that can be tested with the resurrection approach.

Trait evolution

- Longer growing season → altered seed dormancy, response to day length and flowering time
- Increased temperature → change in temperature optima for photosynthesis
- Frequent drought/elevated carbon dioxide → changes in water use efficiency and specific leaf mass
- Altered pollinator communities → changes in floral morphology, breeding system
- Altered herbivore communities → changes in defensive traits
- Altered soil microbial community → change in nutrient requirements and uptake ability
- Shifting climate envelope → increased dispersal ability at leading range edge

Evolution of genetic architecture

- Selection response due to frequency shifts at a few loci of large effect versus many of small effect
- Strong selection responses → reduced genetic variance
- Increased climate variance → increased phenotypic plasticity
- Selection responses constrained by genetic correlations
- Phenotypic evolution through fixation of alleles with positive epistatic interaction
- Differential evolutionary responses among species within a ploidy series

Genomic evolution

- Selection response from novel mutations versus standing variation
- Strong selection on locus → reduced variation at linked neutral loci (selective sweeps)
- Selection response due to functional divergence of duplicate genes

Phylogeography/population genetic structure/extinction

- Low genetic variability → higher extinction probability
- Extinction rates correlated to rate of climate change
- Dwindling population size at leading and trailing edge of range → increased drift
- Neutral markers indicate net direction of dispersal

Because extant lineages within any species are geographically distributed in ways that reflect genealogical connections through near and distant ancestors, space and time are the joint axes of interest in phylogeography (Avise 2000). The resurrection program will facilitate phylogeographic reconstructions. The importance of extensive geographic sampling in comparative phylogeography is illustrated by the successful multinational effort to identify Pleistocene refugia and post-Pleistocene dispersal patterns for numerous plants and animals on the European continent (Weiss and Ferrand 2007).

Summary

Time capsules are a popular way of storing important materials for the future. We propose to create, through Project Baseline, a well-designed time capsule of seeds that will enable future investigators to document microevolution during a period of rapid environmental change. Combining the resurrection approach with quantitative and molecular genetic techniques will allow scientists to document ongoing evolution unequivocally, and will also facilitate efforts to dissect the underlying mechanisms of evolutionary change.

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