Paleoecology and "inter-situ" restoration on Kaua`i, Hawai`i

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Paleoecological studies from tropical islands around the globe show that human colonization has been devastating for these remote biotic communities. Island histories reveal that human predation and human-mediated landscape change have each played a key role, but many island extinctions following human arrival are strongly associated with introduced predators, herbivores, weeds, and diseases. On the Hawaiian Island of Kaua`i, human-caused extinctions are currently occurring in a microcosm of island endemics. Recent studies of endangered plants suggest that conventional in-situ and ex-situ conservation strategies are losing the battle here. Paleoecological findings support the idea that creating new populations in formerly much larger, late prehistoric and early historical ranges of declining species may provide a reliable and cost-effective hedge against extinction. On Kaua`i, several paleoecological sites have played key roles in planning and implementing ecological and cultural restoration projects.

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Biotic collapse appears, without exception, to follow human arrival to remote tropical islands around the world. Although debate continues regarding the causes of late Quaternary extinctions on continents, there is almost universal agreement in the scientific community that humans have been transforming remote tropical oceanic islands at a rapid pace ever since the onset of local human colonization (Steadman 1995; Burney and Flannery 2005).

Direct human predation and deforestation have each been frequently invoked to explain the changes, although both prehistoric evidence and historical records also document indirect effects of humans, including introduced predators, herbivores, alien competitors, and diseases. Human disruption of island biota probably began more than 50 000 years ago in New Guinea, and spread prehistorically to other islands, in the wake of their discovery. The process was directly observed and documented in the later cases, including the Mascarene and Galapagos Islands, where initial human colonization has been a phenomenon of recent centuries (Martin and Steadman 1999; Burney and Flannery 2005).

Perhaps no case of "tropical paradise lost" is more familiar than that of the Hawaiian Islands, first colonized by Polynesians one to two millennia ago. Recent research employing accelerator mass spectrometer ^{14}C dating of materials least likely to be contaminated with old carbon, such as plant macrofossils and purified bone collagen, support the later arrival scenarios, hardly more than 1000 years ago (Athens *et al.* 2002; Burney and Burney 2003). Casualties in the wake of human arrival included large, flightless waterfowl and other ground-nesting birds, and perhaps others (Olson and James 1984). Following Captain Cook's two voyages in 1778–79 and subsequent European colonization, finches, land snails, and plants figured among the major losses on these mid-Pacific volcanic islands.

A complex web of causation can be imagined. Various human impacts interacted with natural variations in climate, demography, and ecological dynamics to drive extreme extinction events, in which many groups were greatly affected or completely eliminated on these and other islands (eg Burney *et al.* 2002; Burney and Flannery 2005). Certain events, such as the introduction of rats (Athens *et al.* 2002), may have had disproportionate effects. In addition, some groups (eg flightless birds) may have been hardest hit, eliminating hundreds or perhaps thousands of species globally (Steadman 1995).

Kaua`i, the oldest and northernmost of the major Hawaiian Islands, is an interesting case for scientists studying human-mediated extinction. The losses have been substantial on Kaua`i, and they are continuing (Burney *et al.* 2001); the extinction catastrophe has not yet finished running its course. An often-cited pair of statistics is that the Hawaiian Islands together represent

In a nutshell:

- Conservation on remote tropical islands demands innovative strategies, as conventional approaches have proved inadequate in many cases
- Paleoecology and other historical techniques may hold solutions for reversing the decline of some endangered species
- These techniques show that many rare species may formerly have had much wider ranges
- The fossil record has been used on Kaua`i, for instance, as a strong justification for creating new populations at sites where intensive management is feasible
- Makauwahi Cave Reserve, a collaboration with Grove Farm Company, has served as a prototype for this approach, defined here as "inter-situ restoration"

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only 0.2% of US land area, but contain 43% of the plants on the endangered species list. Of all the islands, Kaua`i holds the dubious distinction of having the largest number of listed species, including many single-island endemics with total populations in the 1–50 range.

Paleoecological studies based on fossils recovered from ancient caves and marshes on this 1430-km^2 island have yielded a detailed picture of biotic changes before, during, and after human arrival (Olson and James 1982, 1984, 1991, 1997; James and Olson 1991; Burney *et al*. 2001; Burney 2002; Burney and Burney 2003; Burney and Kikuchi 2006). In an unusual development, however, studies of past environmental cataclysms have become a more direct part of contemporary conservation activity than is customary. Although paleoecological insights have led to some interesting and controversial "Pleistocene rewilding" proposals in the North American conservation community and elsewhere (eg Martin 2005; Donlan *et al*. 2005, 2006; Donlan 2007; Caro 2007), Kaua`i hosts numerous ecological restorations that have, with only minor controversy, drawn their inspiration and part of their scientific justification directly from the findings of avian paleontologists, palynologists, archaeologists, and ethnohistorians. An early and spectacular example was the reintroduction of the Nene, or Hawaiian goose (*Branta sandwicensis*), to other islands, including Kaua`i, from a tiny historical population known exclusively from the Big Island.

Surfing the extinction wave

The Hawaiian Islands are ripe for new conservation ideas for several reasons. First, the situation there is dire. The lowlands of Kaua`i, for instance, are almost entirely lacking in native vegetation and suitable habitat for endangered animals. Exotic vegetation blankets the landscape up to elevations of 1000 m or more in many areas, with some notable, but highly threatened exceptions. Thousands of hectares are covered with invasive alien plants; some, such as ratberry (*Rhodomyrtus tomentosa*), Guinea grass (*Panicum maximum*), and haole koa (*Leucaena leucocephala*), form essentially mono-dominant stands that successfully exclude most natives and even many other alien invasives. No native passerine birds are regularly seen below ~ 1000 m, due to the presence of the introduced mosquito *Culex quinquefasciata*, which carries avian malaria and bird pox, introduced diseases apparently fatal to native honeycreepers and other endemic perching birds. Most endemic land snails, including the large, colorful *Carelia* species, are believed to be extinct. Giant flightless waterfowl, the original meso-herbivore community of the islands, have been extinct for centuries (Olson and James 1982, 1984, 1991; James and Burney 1997), and the endemic flying waterfowl, such as the Nene and the Koloa duck (*Anas wyvilliana*), are on the US federal endangered species list.

Second, this dire situation is not getting better for most species, but is instead worsening. In-situ conservation in state and national parks, forest reserves, military reservations, and private holdings has proven to be expensive and difficult to maintain for so many species at once, in the face of major challenges from feral ungulates, introduced predators, invasive plants and invertebrates, and diseases – all exacerbated by the ravages of hurricanes, landslides, pollution, and development. Ex-situ conservation in botanical gardens, native-plant nurseries, arboreta, and seed banks has shown progress, but the extent to which public and private institutions can address the challenge is limited by the costs of labor, greenhouse and garden space, genetic constraints, hybridization, and the absence or scarcity of natural recruitment. Ex-situ strategies have benefited from new ecological and horticultural techniques, but the entire effort is at risk of being swamped by the sheer number of species in decline, the rapidity of their decline, and regulatory hurdles (Holling and Meffe 1996). One study suggests that 590 of the 1209 species of native Hawaiian plants are already extinct or at risk of extinction (Wagner *et al*. 1999).

Formal status reviews of each listed endangered species are just beginning for the long list of Hawaiian plants, but results from 21 species evaluated by the Conservation Department of the National Tropical Botanical Garden (NTBG) in 2006, under contract from the US Fish and Wildlife Service, show the magnitude of the challenge in microcosm: all these species, save perhaps one or two, have declined since their official listing under the Endangered Species Act, most not only in total number, but in number of populations as well (WebTable 1). These species were selected on the basis of administrative considerations (their turn on a 5-year update cycle), not because they were perceived to be at greater risk than others on the list. In nearly all cases, the cause of decline is not known with certainty, but the observed or inferred negative influences are the usual litany – the same factors indicated in the fossil record of island extinctions in the human period (WebTable 1).

Restoration paleoecology

The community of conservation professionals and dedicated volunteers in the state of Hawai`i is sizeable, and many energetic projects are underway. Leading conservationists have recently called not only for a greater effort, but for a more focused, creative approach, based on the best science available and promoting research (Duffy and Kraus 2006). Two ideas in particular have attracted attention at recent regional conservation meetings as possible breakthroughs in addressing the overwhelming challenge. It could be argued that these are simply two sides of the same coin. On one side is the emerging practice of using local paleoecological, archaeological, and ethnohistorical sources to develop restoration plans and propose reintroductions for managed areas (Burney *et al*. 2002); on the other is the emerging concept of inter-situ conservation (See Panel 1; Blixt 1994; Guerrant *et al*. 2004). These two ideas have proven to be highly synergistic, in that, for instance, paleoecological findings are increasingly used to support proposals to create new populations in the late prehistoric and early historical range of declining species. Although the term "inter-situ" has been used in conservation for more than a decade and in several different contexts (see Blixt 1994), we propose here a definition that encompasses most usages (Panel 1).

In practice, most of these projects involve a variable mix of horticultural and agricultural techniques, in which reintroduced species are subsidized for a time, but husbandry is eventually, often gradually, withdrawn. Familiar examples would be "soft-release" techniques for reintroduced animals, and temporary irrigation systems, periodic soil amendments, and weeding for reintroduced plants. Although the site may resemble a barnyard or cropfield initially, the ultimate goal is usually a phased withdrawal of most direct care to the recolonizers (ungulate exclusion fences being a major exception) and a hope for reproduction and recruitment success. A key advantage with most inter-situ projects over more remote in-situ locations is that greater accessibility and a lack of jurisdictional complications make it generally more feasible to correct and continue addressing the challenges that resulted in species' decline in the first place.


Courtesy of Alec Burney

Figure 1. *View of the western wall of the large sinkhole in the center of Makauwahi Cave.* Pritchardia aylmer-robinsonii *palms in the foreground, although extinct on Kaua`i today, were reintroduced to the site from the adjacent island of Niihau because their seeds and pollen were abundant in the pre-human sediments excavated from the site.*

Paleoecology has played a variety of supporting roles in this effort on Kaua`i. First, studies of past ecosystems have shown scientists and the public the full magnitude of extinction losses and ecological transformations that have come in the wake of human disturbance, reinforcing the sense of urgency. Second, information of this type has provided direct scientific justification for efforts to implement corrective measures, such as feral ungulate management and exclusion, increased agricultural inspection controls over incoming materials that might introduce new invasions, and protection of archaeological and historical sites. Third, and perhaps most importantly from the standpoint of ecological theory, paleoecological findings have revealed some surprising details about the formerly much wider ranges of now-rare plants and animals in pre-human Kaua`i and subsequent changes in their environments. Finally, paleoecology, environmental history, and ethnographic information about landscapes and species give interpretive and educational programs a better *sense of place* by providing, in addition, *a sense of time in a place* (WebPanel 1)

■ Makauwahi Cave Reserve: low-cost time travel

Multidisciplinary studies at Makauwahi Cave, Maha`ulepu, on Kaua`i's south shore (Figure 1), first revealed some critical details needed for restoration on the dry, leeward side of the island (Burney *et al.* 2001). Pollen and plant macrofossil results showed unequivocally, for the first time, that pre-human coastal and lowland vegetation was far more diverse than would be guessed from the surviving, degraded patches of native plant communities here. Many species associated today with a few high interior sites of a very different type were, in the pre-human late Holocene, quite typical in these coastal forests. This suggests that ecological restoration at the site, in which alien vegetation is being removed and natives planted in their place, could in fact make use of a much more diverse list of plants than previously imagined, including many at-risk species – some of them among Kaua`i's rarest today. This approach, combining past information with futuristic restoration strategies, is now being tried throughout the island (Figure 2).

The 6.9 ha (17 acres) including and surrounding the Makauwahi Cave site have, through a lease arrangement with Grove Farm Company, become a laboratory for using information from the past to guide ecological and cultural restoration on Kaua`i (Burney *et al.* 2002; Burney and Kikuchi 2006). Six distinct ecological restoration strategies are in use on the landscape (Figure

Panel 1. Three types of conservation: definitions

In-situ: Conservation efforts applied to species in a pre-existing wild condition in their current range.

Ex-situ: Conservation efforts based in intensively human-controlled environments, such as botanical gardens, zoos, genetic banks, and propagation facilities.

Inter-situ: The establishment of species by reintroduction to locations outside the current range but within the recent past range of the species. In some cases, closest living relatives or ecological surrogates may be substituted for globally extinct species that are regarded as essential to maintain a process believed critical to the function of the target ecosystem. Inter-situ conservation, in effect, bridges the gaps between in-situ and ex-situ conservation.

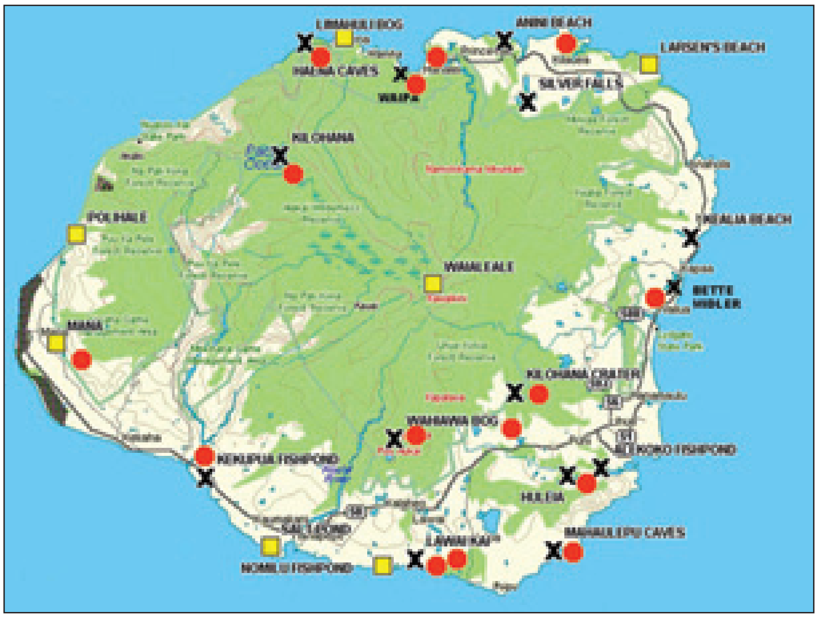

***Figure** 2. Map of Kaua`i showing dated paleoecological sites (**X**), undated sites (yellow boxes), and restoration sites (red dots) that have utilized paleoecological data. Makauwahi Cave Reserve encompasses the Maha`ulepu Caves site and additional abandoned farmlands.*

3), each following guidelines constructed after years of research in palynology, paleontology, archaeology, history, and ethnography focused on the site.

Restoration activities include soil improvement, invasive species control, outplanting of indigenous and endemic plants and Polynesian cultivars, and protection of the cave environment. To date, no animal reintroductions have been undertaken, but fossil taxa from the site that are extinct on Kaua`i but survive elsewhere, and which have been discussed as possible future reintroductions, include the Laysan teal (*Anas laysanensis*), Hawaiian hawk (*Buteo solitarius*), a land crab (*Geograpsus geayi*), and endemic snails and insects (Burney *et al.* 2001, 2002).

Makauwahi Cave contains at least three extremely rare troglobitic (cave-obligate) invertebrates – an amphipod (*Spelaeorchestia koloana*), an isopod (*Hawaiioscia* cf *rotundata*), and a spider (*Adelocosa anops*) – all of which are unpigmented and eyeless. The long subterranean passages were mapped not only underground, but on the cave's footprint (sometimes referred to by cavers as a "headprint") above, on the landscape. Special management of this federally designated, critical habitat for troglobites has included growing native plants above the cave passages, the long roots of which are important to the subterranean food web (Howarth 1973). Plants such as maiapilo (*Capparis sandwichiana*), `uhaloa (*Waltheria indica*), and a`ali`i (*Dodonaea viscosa*) may provide the energy base for this unlit ecosystem. The water-seeking roots of these plants extend to the cave level and produce nutritious exudates that sustain fungi, bacteria, and ultimately, blind invertebrate grazers and the blind spider at the top of this unusual energy pyramid. To our knowledge, this is the first site anywhere in the world to host an ecological restoration of native plants for the ultimate benefit of a subterranean food web, although this has now also been done above two lava-tube systems nearby that host subterranean biota.

Another management unit is the site of inter-situ management at the large end of the spatial scale. A native forest is being reconstructed on abandoned agricultural land formerly devoted to sugar cane and corn. Using the list of "living fossils" as a guide, and drawing on the propagation skills of the staff of the Conservation and Horticulture Center of the nearby National Tropical Botanical Garden (NTBG), researchers are finding that native plants, including some of the rarest species, can be grown in this habitat in large numbers, using tractors and other implements of large-scale farming to do most of the work. Over 1650 plants, representing 77 taxa, have been successfully established on the initial one-hectare (2.5-acre) plot. Overall survival of the nursery-produced plants, which are generally kept on a "life-support system" of automated drip irrigation until well-rooted (roughly 1 year for most native plants), has been 88% (WebTable 2).

Another management unit, a garden in a 0.4-ha (1-acre) sinkhole in the midst of a limestone cave system, is a more intensively managed demonstration garden, featuring many of the plants most abundant around the site just before human arrival, including several that are virtually extinct in the "wild". The thousands of visitors who have toured the site, guided by the researchers, volunteer docents, and trained professional guides, have the unusual triple treat of touring the largest limestone cave system in the state (complete with stalactites and other speleothems – secondary mineral deposits found in cave systems – as well as blind cave creatures), seeing a large-scale working scientific excavation, and witnessing the results of the ecological study of the past applied to restoration, arguably the ecological science of the future (Figure 4). The interpretive program features not only rare plants, blind invertebrates, geological wonders, and applied ecology, but a wealth of cultural elements. The cultural research component of the site includes many perishable artifacts (eg made from wood, plant fibers, gourd shell, and bamboo), 19th-century maps and documents, and ethnographic accounts collected from local elders.

Although the cave has served as a focus for this past/future visualization, many other sites around the island have also played important roles in both paleoecology and restoration activity (Figure 2). At Limahuli Garden and Preserve – a nearly 400-ha (1000-acre) panoramic valley on Kaua`i's north shore, owned and managed by NTBG – ethnohistoric accounts, old photographs, family legends, archaeology, and sediment coring (Burney 2002) have each played a role in developing the management strategy and interpretive program for this spectacular site, featuring centuries-old working agricultural terraces and some of the most pristine native forest surviving on the island.

Other sites (Figure 2; WebTable 3) include prehistoric fish ponds, in-situ habitat rehabilitations, cultural restorations, and large-scale inter-situ plant restorations on private lands, each fortuitously or intentionally sited at or near a paleoecological site that has been used in background studies, planning, and/or interpretation during the restoration. Monitoring programs have, in many cases, been in place for insufficient time to fully evaluate the effectiveness of the project, but the overall prognosis is encouraging.

In short, Kaua`i has emerged as a leader in using paleoecological findings to support the creation of new populations in the late prehistoric and early historical range of rare or declining species. This idea – paleoecologically based inter-situ restoration or, simply, "island rewilding" – is attracting interest from personnel working on other restoration projects throughout the Hawaiian Islands. Elsewhere in the Indo-Pacific region, from South Pacific Islands to New Zealand to Mauritius and Madagascar, conservationists are looking to see what the past can tell them about the future (reviewed in Burney *et al.* 2002; Donlan 2007).

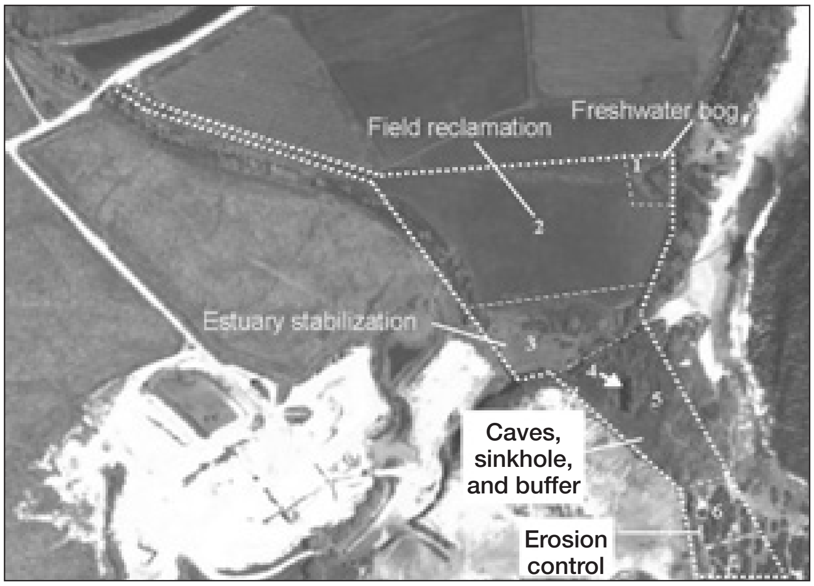

Figure 3. *Aerial photo of the Makauwahi Cave Reserve and environs. Outer dashed line indicates boundaries of Reserve and access right-of-way. Inner dashed lines delineate management units, each with different methods, goals, and challenges for ecological restoration. Unit 1: a small freshwater bog originally containing two native sedges, now enriched with 12 additional species of native wetland plants; Unit 2: an abandoned agricultural field originally containing only one native plant species, now enriched with 77 native and Polynesian-introduced plant species; Unit 3: estuary stabilization project, including erosion control measures and establishment of five native riparian species; Unit 4: demonstration garden inside sinkhole, initially containing one native plant species, now featuring 23 species of native and Polynesian plants, most of them particularly well-represented as fossils in the sediments; Unit 5: sinkhole rim and headprint of the cave passages, initially containing six native species, enriched with 18 more; Unit 6: erosion control area, where control of vehicle damage to the dunes and invasive plants led to the recovery of five native dune species, now enriched by 11 additional natives.*

Present and future plans

How much farther can Kaua`i go with this synthesis of past and future ecology? To what extent can these ideas work in other contexts? These are somewhat philosophical questions, but the answers are essential to defining protocols for conducting this kind of ecological restoration on larger geographic scales. Recent projects underway and proposed for Kaua`i (see WebTable 3) include inter-situ management of areas of 8–12 ha (20–30 acres) or more, on private lands. This entails adapting multi-species native outplantings to the scaled-up demands normally met by agroforestry techniques applied to forest monoculture or low-diversity plantings of thousands of tree seedlings. These mega-projects must deal with the increased labor requirements of larger, managed high-diversity areas, while seeking, through increased mechanization, to minimize the per-hectare manual labor input. Projects are looking to larger volunteer pools (eg Boy and Girl Scout programs on the island), use of more efficient mulching and ground-cover techniques, hands-on educational programs, and other efficient solutions. Increased labor demands are generated by projects with primary goals of high (mostly reintroduced) biodiversity, as well as restoration of ecological function and community dynamics. These are far more complex systems than "reforestation", aimed at merely re-establishing tree cover from one or a few native species.

Standard procedure in all these projects is to conduct baseline studies, to document carefully all restoration treatments and the genetic pedigree of the plant stock used, and to monitor the results. Sites vary in the intensity of monitoring, but most projects include repeat photography stations, digital mapping of plant locations, periodic vegetation sampling, and establishment of manual or automated devices for measuring local weather conditions, water quality, and soil condition. The National Tropical Botanical Garden and Waipa Cooperative, in collaboration with the University of Hawaii researchers and Intelesense Technologies (Honolulu, HI), have established wireless data loggers that report weather and water parameters to a web-accessible database. Implementation of an expanded network including other sites, such as Makauwahi Cave, and other technologies, such as automated time-lapse photography and soil loggers, is currently underway. For example, Tauber traps (static non-overload pollen collectors) at Makauwahi Cave Reserve are used to continuously mon-

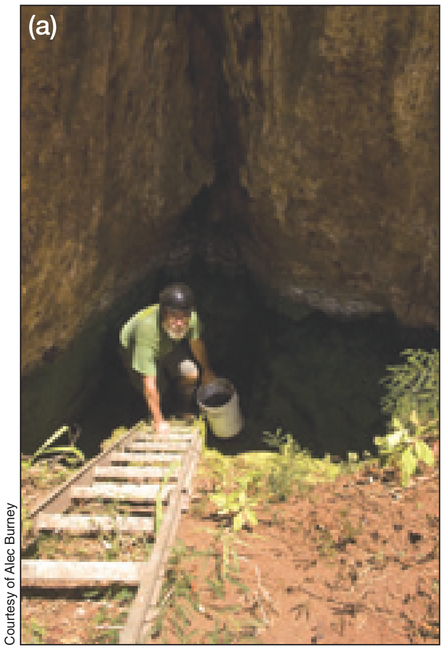

Figure 4. *(a) DAB climbs out of a deep pit with a bucket of excavated sediment containing bones, shells, seeds, and other fossils from extinct and endangered biota of Kaua`i. (b) LPB harvests a seed pod to grow more maiapilo, or Hawaiian capers* (Capparis sandwichiana)*, common as a fossil in the Makauwahi Cave sediments and still growing nearby today. These plants are featured in the restoration unit above the cave because experts on the blind cave biota have found that nutritious exudates on the roots of this plant, which extend into the cave environment, form the base of the troglobitic food web.*

itor the site's airborne particulates in a range of environments.

Experimental arrays of various sorts have been established at a number of restoration sites at NTBG and Makauwahi Cave, to test the efficacy of a range of husbandry techniques for native plants. More of this type of work is planned in the near future, in collaboration with University of Hawai`i graduate students and research scientists. Experimental plots have been established as part of some wetland projects, such as the restoration on Lawai Stream and in Units 1 and 3 of Makauwahi Cave, to determine which native plants can restore ecological functions, for example binding soil on stream banks, competing with invasive marsh and riparian plants, and efficiently providing food and habitat for native waterfowl and wading birds.

Genetic considerations

One of the most interesting future challenges for inter-situ restoration on Kaua`i and elsewhere centers on the role of genetics in decision making. The pioneering work of Soulé and colleagues (eg Gilpin and Soulé 1986) set the standard for including genetic considerations in conservation planning. The possibilities introduced by inter-situ restoration, however, raise important questions and promise a rich harvest of results from large-scale genetic experimentation with reintroduced populations. Whereas this type of work has progressed with animals to the point of genetically enriching small populations (eg panthers and wolves in North America; Caro 2007), techniques for conserving plant genetic diversity are still in their infancy.

For instance, conventional thinking has supported the idea that new plant populations, and tiny relict populations, should be kept genetically "pure" by using only stock from the nearest in-situ population or populations. In the kinds of situations typical for many of the rarest Hawaiian plants, however, the nearest "population" may consist of only one or a very few individuals. In such cases, should we try to create new populations using only a tiny fraction of the potential genetic variation available, or should we create new populations, infused with as much variation as possible? If a new inter-situ population is to be created for a species represented by a nearby in-situ population of two individuals, but three more individuals exist elsewhere on the island, should the new population be started from two or five founders? Even the extremely conservative restorationist would probably opt for capturing the additional variation represented by the larger set, but what if the other three are on another island? What if one population contains 20 individuals, and the other contains 30? Clearly, these are tough questions that have to be evaluated with only limited data.

Paleoecology, however, may provide a surprising amount of insight. For instance, several species used in restoration at Makauwahi Cave and NTBG have widely disjunct populations today, none of which are near the site. But, throughout the Holocene, until the advent of humans (as recently as a millennium ago), these species probably extended across the area between these disjunct populations, based on their occurrence in various fossil sites, including the vicinity of the cave (Burney *et al.* 2001). In other words, present distributions are merely a recent human artifact, so rejoining the anthropogenically disjunct populations would be the most prudent solution. Similarly, since many inter-situ populations are in rather different habitats from any of the modern disjuncts (which are usually on steep cliffs or other rough terrain in the interior, not necessarily because this habitat is more suitable, but because it is the only safe haven from goats and pigs), arguments in favor of preserving narrow genotypes in new populations are overridden by the need to provide maximum variation, so that appropriate phenotypes for the "new" habitat can emerge.

Adaptive management

In reality, the inter-situ strategy will be one of adaptive management, as scientists, horticulturists, and volunteer groups collaborate to learn their way through this local and highly challenging version of the global biodiversity crisis. Well before the quantitative results of most formal experiments are gathered, native-plant growers will have found ecological combinations that work for a given site, through systematic trial-and-error, common sense, and occasional hints from the records of the past. At Makauwahi, for instance, the first appearance in the record of Polynesian-introduced Pacific rats (*Rattus exulans*) coincides with the sudden disappearance of nutritious, thin-shelled seeds of the native *Pritchardia* palms; thick-shelled seeds of *Zanthoxylum* spp, on the other hand, have persisted well past this date. This hints strongly that native palms could only be re-established if there is effective rat control, and the project members have followed this "advice" from the fossil record, through the establishment of rat-free zones. Where this is not feasible, net bags or wire cages are placed over the *Pritchardia* inflorescences, to protect developing seeds.

So far, it is safe to say only that each site poses unique challenges, so that horticultural generalizations are less useful than site-specific knowledge. For instance, it is becoming clear that on drier sites (perhaps < 1500 mm of rainfall per year), certain native ground-cover species can effectively compete with many invasive weeds if given a head start under the right circumstances. Wetter sites, on the other hand, have so far been manageable only with labor-intensive hand removal or mowing – or a scale of long-term herbicide use larger than many professionals would prefer and potentially more disruptive than a large segment of the local public would condone for a "natural" area.

One interesting question for ecologists, conservationists, and resource economists has often been posed by visitors. What are the ultimate fates and purposes of these inter-situ sites on Kaua`i? An obvious motivation is to provide additional habitat to newly created or enhanced populations of native plants, including rare island endemics. This is a given, and the initial results are exciting and gratifying, even in the face of the continued grim crisis of biodiversity loss in Hawai`i. In both theory and practice, however, other uses are emerging, some quite obviously utilitarian.

Extractive reserves

On sites reclaimed from fallow agricultural fields initially lacking native species, such as Makauwahi Unit 2, the planting design and management approach have from inception been geared toward creating a place that will be managed as an extractive reserve. Plants established here, and their offspring, are providing nursery stock for other restorations and gardens, plant products useful to native herbalists, craftsmen, and woodcrafters, taxonomic and genetic study material, and other biological resources to be managed sustainably. One project underway at several NTBG sites and Makauwahi involves production of native plants used in lei-making, including the coveted maile vine (*Alyxia stellata*), currently at risk of over-harvesting in the island's native forests.

In addition to native plants, some restoration sites contain areas that target not pre-human Kaua`i, but early Polynesian times, as a reference system for restoration. At Lawai-kai, for instance, the stated goal of the restoration project is to reconstruct the plant community, inferred from fossil pollen and seed studies in the area, as it might have appeared shortly *after* Polynesian arrival. Thus, some restorations feature plants believed from the fossil and archaeological record, and generally confirmed by traditional lore, to have come in the double-hulled canoes of the founders of the Hawaiian people. Of special interest in this regard are projects that focus on ex-situ or inter-situ preservation of old Hawaiian cultivars or landraces of breadfruit, banana, coconut, sweet potatoes, and that key Polynesian staple crop, taro (*Colocasia esculenta*). Historical documents, ethnographic accounts, and even the rare find of a centuries-old yam tuber in the sediments of Makauwahi Cave (Burney and Kikuchi 2006), support the idea that such root crops were grown in these dry areas in pre-contact Hawai`i.

Figure 5. *At the Grove Farm Ecological Restoration on Kilohana Crater in eastern Kaua`i, hundreds of local Scouts and middle-school students have participated in large-scale inter-situ native plantings guided by paleoecological records of past vegetation nearby.*

Environmental education

These projects have the right mix of aesthetic appeal and informal education to attract a portion of Hawai`i's massive tourist trade, but they also stand up well as high-quality, formal, outdoor education for kindergarten to post-doctoral and adult outreach projects. NTBG sponsors clubs in all the island's high schools – called Junior Restoration Teams (JRT) – that channel interested students into a multi-session training program of up to 8 days per year, in which these young applied ecologists conduct the restoration work described in this article. Last year, over 650 local students participated in this program. By the end of the school year, they had worked through a complete syllabus of field sessions providing on-the-job training in invasive species control, native-plant propagation, cultural-site restoration, stream management, GIS – even paleoecology. JRT members, like other school groups, come to understand fully the meaning of biodiversity loss when they excavate and catalogue sub-fossil plants and animals in Makauwahi Cave, then go out to the field and help to reintroduce many of the same species to their former habitats (Figure 5).

The history of conservation on Kaua`i and elsewhere may show that conservationists bold enough to surf the current extinction wave managed to bring some species back from the brink by buying enough time for these species and communities to benefit from more elegant solutions that scientists may yet discover. Until then, restoration paleoecology may encourage conservationists to cast the widest safety net conceivable for species that are otherwise slipping away.

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■ References

Athens JS, Tuggle HD, Ward JV, and Welch DJ. 2002. Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai`i. *Archaeol Oceania* **37**: 57–78.

Blixt S. 1994. Conservation methods and potential utilization of plant genetic resources in nature conservation. In: Begemann F and Hammer K (Eds). Integration of Conservation Strategies of Plant Genetic Resources in Europe. Gatersleben, Germany: IPK and ADI.

Burney DA. 2002. Late Quaternary chronology and stratigraphy of twelve sites on Kaua`i. *Radiocarbon* **44**: 13–44.

Burney LP and Burney DA. 2003. Charcoal stratigraphies for Kaua`i and the timing of human arrival. *Pac Sci* **57**: 211–26.

Burney DA and Flannery TF. 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends Ecol Evol* **20**: 395–401.

Burney DA, James HF, Burney LP, *et al*. 2001. Fossil evidence for a diverse biota from Kaua`i and its transformation since human arrival. *Ecol Monogr* **71**: 615–41.

Burney DA and Kikuchi WKP. 2006. A millennium of human activity at Makauwahi Cave, Maha`ulepu, Kaua`i. *Hum Ecol* **34**: 219–47.

Burney DA, Steadman DW, and Martin PS. 2002. Evolution's second chance: forward-thinking paleoecologists advocate jump-starting diminishing biodiversity. *Wild Earth* **12**: 12–15.

Caro T. 2007. The Pleistocene re-wilding gambit. *Trends Ecol Evol* **22**: 281–83.

Donlan CJ. 2007. Restoring America's big, wild animals. *Sci Am* **296**: 70–77.

Donlan CJ, Greene HW, Berger J, *et al*. 2005. Rewilding North America. *Nature* **436**: 913–14.

Donlan CJ, Berger J, Bock CE, *et al*. 2006. Pleistocene rewilding: an optimistic vision for 21st century conservation. *Am Nat* **168**: 660–81.

Duffy DC and Kraus F. 2006. Science and the art of the solvable in Hawai`i's extinction crisis. *Environ Hawaii* **16**: 3–6.

Gilpin MA and Soulé ME. 1986. Minimum viable populations: processes of species extinction. In: Soulé ME (Ed). Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer Associates.

Guerrant Jr EO, Havens K, and Maunder M. 2004. Ex-situ plant conservation: supporting species survival in the wild. Washington, DC: Island Press.

Holling CS and Meffe GK. 1996. Command and control and the pathology of natural resource management. *Conserv Biol* **10**: 328–37.

Howarth FG. 1973. The cavernicolous fauna of the Hawaiian lava tubes. 1. Introduction. *Pac Insects* **15**: 139–51.

James HF and Burney DA. 1997. The diet and ecology of Hawai`i's extinct flightless waterfowl: evidence from coprolites. *Biol J Linn Soc* **62**: 279–97.

James HF and Olson SL. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part II. Passeriformes. Washington, DC: American Ornithologists' Union.

Martin PS. 2005. Twilight of the mammoths: Ice Age extinctions and the rewilding of America. Los Angeles, CA: University of California Press.

Martin PS and Steadman DW. 1999. Prehistoric extinctions on islands and continents. In: MacPhee RDE (Ed). Extinctions in near time: causes, contexts, and consequences. Tucson, AZ: University of Arizona Press.

Olson SL and James HF. 1982. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before Western contact. *Science* **217**: 633–35.

Olson SL and James HF. 1984. The role of Polynesians in the extinction of the avifauna of the Hawaiian Islands. In: Martin PS and Klein RG (Eds). Quaternary extinctions: a prehistoric revolution. Tucson, AZ: University of Arizona Press.

Olson SL and James HF. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part I. Non-Passeriformes. Washington, DC: American Ornithologists' Union.

Olson SL and James HF. 1997. Prehistoric status and distribution of the Hawaiian hawk (*Buteo solitarius*), with the first fossil record from Kauai. *Bishop Museum Occasional Papers* **49**: 65–69.

Steadman DW. 1995. Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science* **267**: 1123–31.

Wagner WL, Bruegmann M, Herbst DR, and Lau JQ. 1999. Hawaiian vascular plants at risk, 1999. *Bishop Museum Occasional Papers* 601–69.

WebPanel 1. Roles for paleoecology in island ecological restoration

- **Context.** Studies of past ecosystems show scientists and the public a fuller picture of the magnitude of extinction losses and ecological transformations resulting from human arrival.

- **Justification.** Information from paleoecology has provided direct scientific justification for efforts to implement conservation measures, such as feral ungulate management and exclusion, rat control, increased agricultural inspection measures, incipient plant interceptions, and protection of archaeological and cultural sites.

- **Detail.** Paleoecological findings have revealed that many currently rare and geographically restricted species were once widespread, providing direct support for inter-situ management strategies aimed at reintroducing species to their former range.

- **Chronology.** Paleoecology, environmental history, and ethnographic information about landscapes and species give interpretive and educational programs a better *sense of place* by providing, in addition, *a sense of time in a place*.

WebTable 1. Conservation status of 21 Hawaiian endangered plant species

Plant	*Status in situ*	*Ex-situ conservation?*	*Inter-situ conservation?*	*Cause(s) of decline*	*Comments*
Acaena exigua	Declining	No	No	Unknown	Possibly extinct; may still exist on west Maui; has been "rediscovered" several times in past 135 years; suitable habitat still exists
Brighamia insignis	Declining	Yes	Yes	Goats, loss of pollinator, invasive plants, fungal disease, rats, slugs	Only one plant left in the wild; many seeds and plants at NTBG nursery; outplantings at several sites
Brighamia rockii	Declining	Yes	Yes	Goats, loss of pollinator	Outplanting at Kalaupapa National Historical Monument Area
Cyanea dunbariae	Declining	Yes	No	Pigs, invasive plants, slugs, rats	Little success in growing plants; seeds are stored at Lyon and NTBG
Cyanea macrostegia gibsonii	Declining	No	No	Rats, slugs, deer	Neither seeds nor basal cuttings have been propagated
Cyanea procera	Declining	No	No	Unknown	No success storing seeds or propagating; landslides, washouts, and hurricanes are threats
Cyanea undulata	Declining	No	No	Pigs, invasive plants, rats, slugs	Hurricanes opened up pristine areas to invasion by invasive plants; floods and landslides
Delissea rhytidosperma	Extinct in wild	Yes	Yes	Pigs, goats, deer, invasive plants, slugs, rats	Successful outplantings in inter-situ restorations
Diellia pallida	Declining	Yes	Yes	Goats, pigs, deer, invasive plants, fungal disease	Fencing needed for existing populations
Gardenia brighamii	Declining	Yes	Yes	Loss of habitat, pigs, deer, sheep, game birds, coffee twig borer, rats, fire	Outplanting problematic because of insect pests
Hedyotis schlechtendahliana remyi	Declining	Yes	No	Possibly deer	Synonym *Kadua cordata remyi;* considered extinct in wild; 32 plants from rooted cuttings at NTBG nursery
Hibiscus clayi	Same	Yes	Yes	Invasive plants, insect pests	Many inter-situ outplantings; 15 in-situ outplantings
Isodendrion pyrifolium	Declining	Yes	Yes	Rats, invasive plants, development	Drought and fire are threats
Kanaloa kahoolawensis	Declining	Yes	No	Drought, mice	Propagation attempts have so far been unsuccessful
Lysimachia maxima	Declining	Yes	No	Pigs, goats, rats, invasive plants	Hurricanes and landslides are threats; twig borers kill nursery plants
Melicope mucronulata	Declining	Yes	No	Coffee twig borer, invasive plants, pigs, goats, deer, rats	Hurricanes and landslides are threats
Panicum niihauense	Same?	Yes	Yes	ATVs, invasive plants	Seeds being collected, stored, and propagated at NTBG
Phyllostegia waimeae	Declining	Yes	No	Pigs, goats, rats, invasive plants	"Rediscovered" in 2000; last observation before "rediscovery" occurred in 1969

(Continued)

WebTable 1. Conservation status of 21 Hawaiian endangered plant species (*continued*)

Plant	*Status in situ*	*Ex-situ conservation?*	*Inter-situ conservation?*	*Cause(s) of decline*	*Comments*
Pritchardia viscosa	Declining	Yes	Yes	Rats, illegal tree and seed collecting, pigs, invasive plants	There has been no enforcement of the laws preventing illegal seed collection and sales
Silene alexandri	Declining	No	No	Goats, competition with non-native plants, loss of reproductive vigor	Difficult to grow, recovery goals for reintroduction have not been met
Viola helenae	Declining	No	No	Ungulates (particularly pigs), landslides, invasive plants	Fruits dehisce explosively, making mature fruits hard to collect; no successful propagation from seeds has been recorded

WebTable 2. Makauwahi Cave Reserve Management Unit 2 (field reclamation) plants represented by > 5 individuals

Plant species	*Reason for including*	*Range*[1]	*Status in 1999*[2]	*Listings status*	*% surviving (n)*[4]
Acacia koaia	Fossil	E	Vulnerable	None	83 (101)
Achyranthes mutica	Historically nearby	E	Endangered	SOC	50 (8)
Bobea timonioides	Historically nearby	E	Rare	SOC	36 (8)
Brighamia insignis	Historically nearby	E	Endangered	Endangered	75 (8)
Callophyllum inophyllum	Grows nearby	P	None	None	88 (8)
Chenopodium oahuense	Fossil	E	Apparently secure	None	93 (28)
Cocos nucifera	Fossil, grows nearby	P	None	None	93 (27)
Colubrina asiatica	Grows nearby	I	Apparently secure	None	100 (13)
Cordia subcordata	Fossil	I	Apparently secure	None	100 (65)
Delissea rhytidosperma	Grows nearby	E	Endangered	Endangered	57 (7)
Diospyros sandwicense	Fossil	E	Apparently secure	None	82 (11)
Dodonaea viscosa	Fossil, grows nearby	I	Apparently secure	None	77 (71)
Erythrina sandwicensis	Grows nearby	E	Apparently secure[3]	None	98 (49)
Gossypium tomentosum	Historically nearby	E	Vulnerable	None	100 (16)
Hibiscadelphus distans	Historically nearby	E	Endangered	Endangered	95 (22)
Hibiscus brackenridgei	Historically nearby	E	Endangered	Endangered	83 (6)
Hibiscus clayii	Historically nearby	E	Endangered	Endangered	95 (20)
Hibiscus waimeae waimeae	Historically nearby	E	Apparently secure	None	86 (22)
Kokia kauaiensis	Fossil	E	Endangered	Endangered	100 (6)
Metrosideros polymorpha	Fossil	E	Apparently secure	None	47 (34)
Munroidendron racemosum	Grows nearby	E	Endangered	Endangered	83 (41)
Myoporum sandwicense	Fossil	I	Apparently secure	None	100 (70)
Nototrichium sandwicense	Historically nearby	E	Apparently secure	None	83 (12)
Ochrosia kauaiensis	Fossil	E	Rare	SOC	54 (13)
Pandanus tectorius	Fossil, grows nearby	I	Apparently secure	None	94 (31)
Pritchardia napaliensis	Fossil	E	Endangered	Endangered	100 (9)
Psydrax odorata	Fossil	I	Apparently secure	None	80 (45)
Rauvolfia sandwicensis	Fossil	E	Apparently secure	None	80 (10)
Reynoldsia sandwicensis	Similar habitat	E	Rare	None	80 (10)
Sapindus oahuensis	Fossil	E	Apparently secure	None	88 (26)
Scaevola taccada	Fossil, grows nearby	I	Apparently secure	None	100 (70)
Sophora chrysophylla	Similar habitat	E	Apparently secure	None	50 (6)
Thespesia populnea	Grows nearby	I?	Apparently secure	None	100 (6)
Wikstroemia oahuensis	Fossil, grows nearby	E	Apparently secure	None	100 (9)

Notes: [1]E = endemic, I = indigenous, P = Polynesian introduction, SOC = species of concern; [2]From Wagner *et al.* (1999); [3]*Erythrina* currently under attack by a new invasive insect, the *Erythrina* gall wasp (*Quadrastichu erythrinae*); status may now be less secure; [4]% surviving defined as % still living 6 months after transplantation; n defined as total number of individuals planted

WebTable 3. Restoration sites on Kaua`i associated with paleoecological studies

Project	*Goals*	*Institution*	*Paleoecological role*	*Status*
Alaka`i Swamp	Build ungulate fence, control invasive species, protect watershed, enhance in-situ populations	Multi-agency, multi-institutional collaboration on state lands	Pollen studies of sediment cores provide 15 000-year background on vegetation, soils, and climate dynamics	Background studies near completion, puaiohi (native thrush) reintroduced, invasive plant and pig control programs underway
Alekoko Fishpond	Restore fishpond and control invasives	Currently for sale, part of federal study	Coring has established age and prior history	National Historic Landmark, but no restoration or active interpretation at present
Grove Farm Ecological Restoration	Create an inter-situ restoration project modeled on Makauwahi Cave restorations	Grove Farm Company, in collaboration with NTBG and University of Hawaii	Pollen studies from Makauwahi, Kilohana Crater, and Kawaihau provide guidance for plant choices	Large-scale restoration underway, labor provided by scouting programs and local schools
Kaua`i National Wildlife Refuges	Provide habitat for native birds and plants	US Fish and Wildlife Service	Fossil record of Nene and native plant occurrences provided justification for reintroductions, Laysan Teal under consideration	Ecological restoration projects underway in all three Refuges (Hanalei, Kilauea, Huleia), Nene now common throughout Kaua`i (700+ wild individuals)
Kawaihau Wetland	Restore wetland for native water birds	Privately owned (Bette Midler Family Trust)	Pollen analysis of sediment cores provides 7000-year background for restorations	Background studies completed, only pilot restorations to date
Kekupua Fishpond	Restore fishpond and establish native vegetation	Robinson Family Partners	Coring provides background on age of pond and earlier vegetation	Studies for ecotourism project completed, work stalled pending implementation funds
Lawai Gardens	Integrate restorations with public gardens	NTBG NTBG	Paleoecological research at Lawai-kai and other south-shore sites	Four types of restorations demonstrated on site, guided tours, education and research
Limahuli Garden and Preserves	Enrich degraded remnant forests, interpret plant conservation	NTBG	Ethnohistorical research, paleoecological and archaeological studies	Mostly in-situ and ex-situ projects, but lowland forests have benefited from inter-situ approach to species enrichment
Makauwahi Cave	Test wide range of restoration methods	NTBG/Grove Farm collaboration	On-site fossils and ethnohistorical research guide restoration choices	Six types of restorations demonstrated on site, guided tours, education and research
Mt Kahili Restoration	Create a fully mechanized, large-scale inter-situ restoration	Hawaii Mahogany Company, in collaboration with NTBG	Paleoecological data from Kilohana Crater and Wahiawa Bog used to generate plant list	Stalled at permitting stage, funding in place, implementation slated to begin in November of 2007
Wahiawa (Kanaele) Bog	Build ungulate fence, control exotics, enhance bog flora	The Nature Conservancy	Core from site provides background information back to late Pleistocene	Environmental assessment complete, work to commence soon on fence
Waipa Restoration	Restore fishpond and establish native vegetation	Waipa Farmer's Cooperative	Coring of fishpond and other sites on property for dating and sedimentological data	Restoration projects provide educational opportunities and cultural experiences