Ecological Change on California's Channel Islands from the Pleistocene to the Anthropocene

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Historical ecology is becoming an important focus in conservation biology and offers a promising tool to help guide ecosystem management. Here, we integrate data from multiple disciplines to illuminate the past, present, and future of biodiversity on California's Channel Islands, an archipelago that has undergone a wide range of land-use and ecological changes. Our analysis spans approximately 20,000 years, from before human occupation and through Native American hunter–gatherers, commercial ranchers and fishers, the US military, and other land managers. We demonstrate how long-term, interdisciplinary research provides insight into conservation decisions, such as setting ecosystem restoration goals, preserving rare and endemic taxa, and reducing the impacts of climate change on natural and cultural resources. We illustrate the importance of historical perspectives for understanding modern patterns and ecological change and present an approach that can be applied generally in conservation management planning.

Keywords: conservation, historical ecology, novel ecosystems, restoration

Earth's biodiversity and ecosystems are changing rapidly, driven largely by human activities, and fueling the assertion that we now live in the *Anthropocene*, an epoch dominated by human influence (see Crutzen 2002). To understand and address modern environmental challenges, researchers increasingly recognize the need for new data and approaches, including contributions from the social sciences, humanities, and Earth sciences (Foster et al. 2003, Lyman 2006, Willis and Birks 2006, Sörlin 2012). An important aspect of this research is *historical ecology*—broadly defined here as the use of paleobiological, archaeological, and historical data to understand long-term ecological change and to provide context for conservation (Swetnam et al. 1999, Rick and Lockwood 2013).

Historical ecology has been applied to terrestrial and aquatic ecosystems around the world and helps provide baselines that may serve as targets for restoration, establish desired future conditions, and aid in the evaluation of long-term ecosystem responses to anthropogenic disruptions and climate change. For instance, patterns of historical land cover in California's Silicon Valley prior to significant European and American modification were used to set restoration targets in a densely populated and modified area (Grossinger et al. 2007). Similarly, McClenachan and colleagues (2012) synthesized the ways that historical ecological data are being used in marine conservation, including setting baselines and priorities for fisheries management and assessing extinction risk. Despite these and other examples, questions remain about how best to use historical data to help manage biodiversity in a dynamic and uncertain global system. Do historic and prehistoric environmental reconstructions provide useful baselines for setting restoration goals, especially considering that, in most cases, we can never completely return to past conditions? Can an understanding of long-term human–environment interactions and legacies of land use help guide future management?

We use California's Channel Islands as a model system to evaluate these questions, to demonstrate the power of interdisciplinary research to improve our understanding of long-term changes in island ecology and biodiversity, and to guide conservation management decisions. The Channel Islands have been shaped by a variety of ancient and modern land uses, including Native American hunting and gathering, commercial ranching and fishing enterprises, national

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Figure 1. The time periods and transitions discussed in this study. These transitions highlight major environmental and cultural transformations of each period (the shaded areas depict the location of the time period on a time line). Photographs (from the top): Bill Faulkner, National Park Service; Todd J. Braje; National Park Service; Desiree Cassell, National Park Service.

defense, tourism, and conservation. Today, the Channel Island ecosystems are widely considered to be degraded and in need of restoration. Effectively and efficiently managing those ecosystems will be increasingly challenging in a future dominated by funding constraints, climatic change, ecological novelty, and other anthropogenic perturbations. We show how a more-than-20,000-year record of ecological, climatic, and anthropogenic change can provide information relevant to contemporary conservation management decisions (figure 1).

Study system

The eight California Channel Islands are located between 20 and 98 kilometers off the southern California coast and range in size from 2.6 to 250 square kilometers. Five of the islands (Anacapa, Santa Cruz, Santa Rosa, San Miguel, and Santa Barbara) are managed by the US National Park Service. One (Santa Cruz) is partially owned and managed by The Nature Conservancy; two (San Clemente and San Nicolas) are managed by the US Navy; and one (Santa Catalina) has three private land owners, with 88% of the island managed by the Catalina Island Conservancy. Each of these groups has a different mission, including national defense, conservation, and recreation, although they all seek to balance other uses with conservation. Therefore, the islands differ in the scale and scope of current human use intensity: Santa Catalina is a tourism destination and has a small city; San Clemente and San Nicolas are home to military installations and training areas with substantial human populations; and the other islands have a visitation mission, but their primary purpose is conservation, and there are no permanent human residents.

Some of the earliest evidence of coastal human occupation of the Americas (some 13,000 years ago) has been discovered on the Channel Islands (Erlandson et al. 2011). During the earliest human colonization, the island ecosystems were markedly different from their current state, with substantially lower sea level and greater forest cover. We know little about the first islanders until about 12,000 years ago, when the earliest residential sites provide glimpses of sophisticated hunting technologies and a diverse subsistence economy focused on shellfish, fish, marine mammals, seabirds, and waterfowl (Erlandson et al. 2011). Ancient human populations reached their peak during the Late Holocene (3500–150 years ago), when the Native Americans on some islands coalesced into large multifamily communities and developed a complex intervillage economic system and trade network between the islands and the mainland (Rick et al. 2005). Native Americans strongly influenced the Channel Island environments for millennia, including using fire to clear vegetation; destabilizing and stabilizing dune ecosystems; imposing strong predation pressure on intertidal shellfish, seals, sea lions, and sea otters; and translocating dogs and perhaps other animal and plant taxa (see nderson RS et al. 2010, Erlandson and Rick 2010). Some of these ancient effects on the structure and character of island ecosystems and landscapes persist today.

Although the ecological impacts of the first Channel Islanders were significant, their scale was fundamentally different from the changes that occurred during the late eighteenth to the early twentieth century, when island ecosystems and indigenous peoples were devastated by European settlers, the fur trade, and commercial ranching enterprises. A maritime expedition led by Spanish explorer Juan Rodríguez Cabrillo wintered on the Channel Islands in 1542–1543 and was followed by other European expeditions. European contact introduced diseases and caused a demographic collapse of Native American populations, and the last indigenous islanders were removed to mainland Spanish missions during the 1820s. In the early 1800s, Russian, Native Alaskan, and other hunters visited the islands and decimated the sea otter, seal, and sea lion populations. Chinese and other fishermen began a lucrative abalone fishing and processing industry by the 1850s. Rats were introduced accidentally by historical shipwrecks on four of the eight islands. Ranchers introduced livestock and other nonnative animals to all of the islands during the 1800s and 1900s, and overgrazing, drought, and flawed management practices led to widespread erosion, the introduction and spread of exotic plant species, and the disappearance of native flora and fauna (see Johnson DL 1980, Corry and McEachern 2009). Ranch management practices improved during the twentieth century, but substantial damage to island soils and vegetation had already occurred. Military use of the islands began in the 1930s and accelerated with the onset of World War II. Military bases are still highly active today on San Nicolas and San Clemente, including shore bombardment on the latter.

Reversing the rapid, extensive, and well-documented ecological effects of the ranching era are the primary focus of current terrestrial vegetation restoration efforts on the Channel Islands. In recent decades, managers have removed most introduced vertebrate herbivores (e.g., sheep, cattle, pigs, deer, goats, elk), and dramatic vegetation changes have followed the release from herbivory (e.g., Cohen et al. 2009). A question now facing island managers is *what next?* Here, we address this question by focusing on three interrelated conservation issues facing these managers: (1) setting ecosystem restoration goals, (2) protecting rare and endemic taxa, and (3) reducing the threats posed by climate change.

Setting vegetation restoration goals

Habitat restoration on the Channel Islands is principally focused on returning ecosystems to their condition prior to the ranching era. However, we do not know precisely what terrestrial plant communities were like after millennia of Native American occupation and the climatic shifts that preceded ranching (Anderson RS et al. 2010). Moreover, the responses of current island ecosystems to the environmental changes predicted for the coming decades are unclear. Biologists and managers in many areas of the world are grappling with similar issues of fragmentary historical data and uncertain future effects of anthropogenic disturbances. We draw on recent paleoecological research on the northern Channel Islands to provide insight into plant communities, species abundance, and fire history during the past 20,000 years (see figure 1).

The plant communities on the islands during the last glacial period were probably dominated by forest or woodland habitats more characteristic of modern environments along the northern California coast (Anderson RL et al. 2008). Sedimentary records on Santa Cruz Island document Douglas fir (*Pseudotsuga menziesii*), Gowen cypress (*Cupressus goveniana*), and bishop pine (*Pinus muricata*), with a diverse understory between about 17,000 and 13,000 years ago. A similar flora was found in contemporaneous sites on Santa Rosa (Kennett et al. 2008), and Late Pleistocene (or older) carbonate (caliche) tree trunks, fossil cones, and pollen from San Miguel also document times when forest and woodland were more widespread (Johnson DL 1977, West and Erlandson 1994). Pollen recovered from marine cores in the Santa Barbara Basin

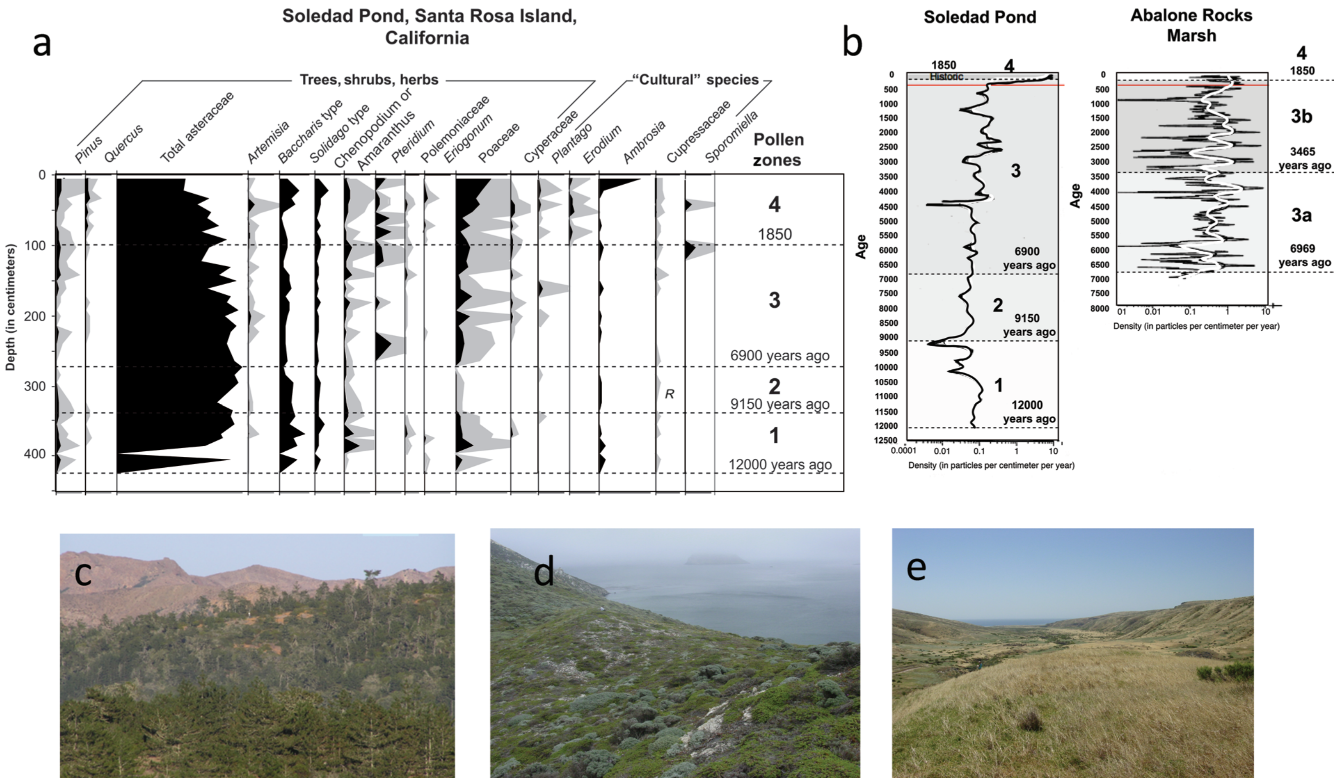

Figure 2. (a) Pollen and (b) charcoal records from the Channel Islands showing long-term changes in vegetation and fire history. Source: Adapted from R. S. Anderson and colleagues (2010). In panel (a), the percentage of pollen is shown in black, and a 10-times magnification projection is shown in gray. The photos show modern Channel Island ecosystems that typify (c) island forest (photograph: Douglas T. Fischer), (d) native-dominated coastal sage scrub (photograph: Torben C. Rick), and (e) island grasslands (photograph: Torben C. Rick).

is also consistent with forested conditions during the Late Pleistocene (Heusser and Sirocko 1997).

Information on the archipelago's Holocene terrestrial plant communities comes primarily from Santa Rosa Island's Soledad Pond (from about 12,000 years ago) and Abalone Rocks Marsh (from around 7000 years ago) (figure 2; Anderson RS et al. 2010). By approximately 11,800 years ago, pine stands were largely replaced by coastal sage scrub and herbs or grassland as the climate warmed and became increasingly dry, particularly after approximately 9150 years ago; fires may have burned more regularly during this transition. As the Holocene progressed, wetlands dried, coastal sage scrub and chaparral covered hillslopes, and fire frequency decreased. By about 6900 years ago, both Santa Rosa sites suggest that perennial herbs and grasses were the dominant vegetation type. Wetland plants became prominent at the upland Soledad Pond and the more coastal Abalone Rocks Marsh site by approximately 4500 years ago as effective precipitation increased. Diatoms suggest freshening of the Abalone Rocks Marsh somewhat later, probably by additional runoff from the highlands. Collectively, these vegetation records document a shift from forested environments during the Late Pleistocene to mosaics of grassland, shrubland, and woodland during the Holocene and modern era, with humans increasingly shaping the composition of plant communities during the nineteenth and twentieth centuries.

Charcoal increased in northern island sedimentary sequences around 3500 years ago, which suggests greater fire frequency (Anderson RS et al. 2010). This pattern has been attributed to intensified Native American landscape burning, which may have had important consequences for island plant communities. Burning by the Chumash has been documented on the adjacent California mainland, but no records exist for the Channel Islands (Timbrook et al. 1982), because ethnographers generally focused on the mainland. Consequently, charcoal records are the main source of evidence of potentially significant prehistoric burning by humans on the Channel Islands. Charred paleobotanical remains from archaeological sites are also an underexplored source of information on ancient island plant communities and human plant-harvesting patterns. More research is needed on these topics, but Native Americans may have shaped island plant communities through burning and activities associated with gathering and processing wild plant foods. They may have also translocated plant species from the mainland or other islands and tended edible wild species, such as oaks and blue dicks

(*Dichelostemma capitatum*), as they did elsewhere in California (see Anderson MK 2005).

During the ranching era (the mid-1800s through the late 1900s), a variety of domestic animals was introduced to different islands, including sheep, goats, cattle, horses, donkeys, pigs, and cats, as well as game species (deer, elk, bison, and turkey). These animals, along with the use of woody plants for firewood and fence building, dramatically altered the island ecosystems, replacing vast areas of the dominant native perennial scrub with nonnative annual grasslands. Overgrazing and livestock trampling caused massive erosion and the loss of organic soil layers (Johnson DL 1980, Anderson RS et al. 2010). On Santa Cruz Island, for example, sedimentation rates increased from approximately 0.4 to approximately 25 millimeters per year shortly after sheep were introduced in 1853 (Perroy et al. 2012). Some native plant populations were relegated to small areas inaccessible to livestock (McEachern and Wilken 2011). These changes set many island endemics on population trajectories that resulted in their decline and endangerment. At least 10 endemic plants have been lost from the islands they once inhabited. Plant population demographic studies identify dysfunction at many life-history stages across taxa, including the loss of pollinators, propagule and seed bank depletion through a century of livestock browsing, the inability of seedlings to compete with nonnative grasses, the lack of protective shading for understory plants from native trees and shrubs, and the loss of whole populations to erosion and grazing (e.g., Junak et al. 1995, Levine et al. 2008, Wilken and McEachern 2011).

The removal of grazing animals from most of the islands during the past four decades has facilitated the recovery of native vegetation and increased the abundance of several endemic plants (e.g., Junak et al. 1995, Corry and McEachern 2009). Soil stabilization has been particularly profound on San Miguel, which has been free of introduced herbivores for over 40 years. Moisture harvest from fog is a major source of water in coastal California ecosystems, and increasing higher-stature vegetation results in more fog capture and drives a restorative feedback process (Carbone et al. 2013). Nevertheless, nonnative grasslands remain a pervasive vegetation type on the islands, differing in structure and function from the native shrublands they displaced.

Looking forward, the long and complex history of vegetation change on the Channel Islands makes setting restoration goals a challenge. The removal of habitat-altering nonnative species is an obvious goal; beyond that, managers have multiple strategies and a variety of possible baselines to consider. For example, the recovery of native woody vegetation will influence the distribution and abundance of endemic grassland and shrubland species. Open habitats will decline as chaparral and woodland communities recover to preranching levels. These changes will be more apparent in the absence of burning by Native Americans, especially if natural wildfires are suppressed. The suitability of annual grasslands as habitat for some grassland-dependent species depends on ongoing management of thatch. Managers may decide to use fire as a management tool to maintain some amount of native perennial bunchgrass habitat in the future.

In setting vegetation management goals, managers must account for the predicted climate warming and changes in precipitation patterns over the coming century (e.g., Cayan et al. 2008). However, impacts on the islands are difficult to forecast because of the uneven effects of climate change on ocean and land areas (e.g., Snyder et al. 2003) and the uncertain and variable gradation of marine and terrestrial effects forecast through the twenty-first century. The profound influence of marine conditions evident in nearshore historical instrumental and proxy climate records demonstrates that both natural change and anthropogenic change have been major components of Channel Island ecosystems for millennia. Therefore, a goal of restoration efforts should be to enhance the *resilience*—the ability to recover relatively quickly from a disturbance—of the archipelago's natural communities to better cope with potentially novel future environments. Managing for resilience would, for example, prioritize the reestablishment and maintenance of a mosaic of complex, diverse ecosystems (Mori et al. 2013). In some cases, unmanaged "natural" vegetation succession may lead to that outcome. In others, managers may need to help foster the desired ecological characteristics through active management.

Protecting endemic taxa

The Channel Islands are home to unique biota of conservation concern. Understanding the patterns of endemism and community composition across this archipelago requires an examination of both natural and cultural histories. The islands have been situated approximately where they are today since the beginning of the Pleistocene, with tectonic uplift and glacial–interglacial changes in sea level periodically increasing and decreasing island sizes. During glacial periods, when the sea level was lower, the islands were larger and effectively closer to the mainland and each other, with important implications for colonization and extinction rates (MacArthur and Wilson 1967). In contrast, sea levels rose significantly during interglacial periods, including during the past 20,000 years, from the last glacial maximum to the present, which resulted in the loss of about 70% of the land area for the islands (figure 3; Muhs et al. 2012). The four northern islands were connected into one landmass, Santarosae Island, until approximately 10,000–9000 years ago, when it separated into four distinct islands (Kennett et al. 2008, Muhs et al. 2012).

The breakup of Santarosae had important effects on Channel Island mammals. The archipelago is currently home to 10 endemic island mammal subspecies (four species, excluding bats; table 1). These include the spotted skunk (*Spilogale gracilis amphiala*), found today on Santa Cruz and Santa Rosa islands, and different subspecies of island fox (*Urocyon littoralis*), found on all of the islands except

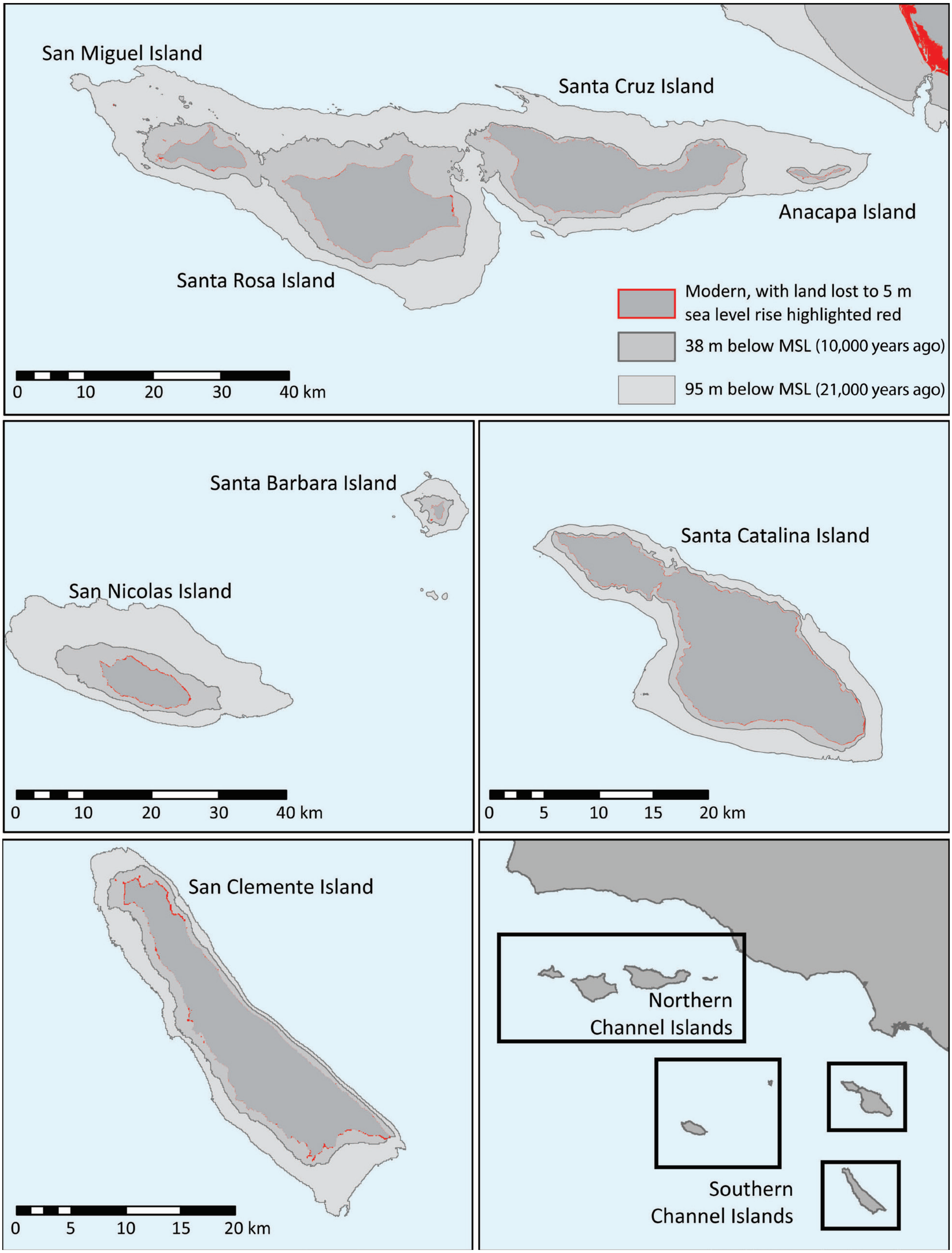

Figure 3. The location of the Channel Islands and approximate changes in land area from sea level rise 21,000 years ago; 10,000 years ago; today; and 100 years from now. Geographic information system modeling of changing sea levels was performed using isostatic adjusted sea level rise models and National Oceanic and Atmospheric Administration and National Geographic Data Center bathymetric data sets. Abbreviations: km, kilometer; m, meter; MSL, mean sea level.

Table 1. Endemic taxa of terrestrial plants and vertebrates on California's Channel Islands.

Island	Plants	Herptiles	Birds	Mammals	Total
San Miguel	19	2	7	2	30
Santa Rosa	43	3	8	3	57
Santa Cruz	52	3	8	4	67
Anacapa	24	1	7	1	33
Santa Barbara	17	1	4	1	23
San Nicolas	17	1	3	2	23
Santa Catalina	37	0	10	5	52
San Clemente	62	1	10	2	75

Note: The faunal counts include extirpated species, and some species occur on multiple islands. These data are based on N. K. Johnson (1972), Power (1994), *www.sbbg.org/conservation-research/channel-islands, www.centerforplantconservation.org/collection/NationalCollection.asp.*

Anacapa and Santa Barbara. Columbian (*Mammuthus columbi*) and pygmy (*Mammuthus exilis*) mammoths lived on the northern Channel Islands until about the time humans arrived (13,000 years ago; see Agenbroad 2012), but we have no definitive evidence that humans killed or scavenged mammoths, and it is possible that habitat loss and a reduction in food supply caused by sea level rise may have played a role in their extinction. One of the smallest island mammals, *Peromyscus nesodytes* (the giant island deer mouse), which has been present on the northern islands for over 40,000 years (Rick 2013), also saw its populations fragmented by rising sea level. Long-term competition from deer mice (*Peromyscus maniculatus*), probably introduced by Native Americans around 10,000 years ago, and habitat alterations led to their extinction by approximately 1000 years ago (Ainis and Vellanoweth 2012). Sea level rise may also have fragmented populations of island spotted skunks on the northern Channel Islands, which may have resulted in genetic differentiation, but questions remain about the timing of skunk colonization (Floyd et al. 2011).

Island foxes provide an example of how changes in sea level and past human activity shaped the evolutionary histories of Channel Island wildlife. The precise date and mode of colonization (natural, human translocation, or a combination) of foxes on the Channel Islands is still debated. Recent evidence suggests a Holocene (i.e., less than 10,000 years ago) arrival for foxes (Rick 2013). Sea level rise may have fragmented fox populations, if they existed on Santarosae, and may have resulted in some genetic differentiation. Radiocarbon dating of what had been hypothesized to be Pleistocene fox remains has produced no evidence of their arrival prior to 8000–7000 years ago, long after the breakup of Santarosae (Rick 2013). Although the isolation of populations on individual islands may have led to distinct populations, Native Americans probably transported foxes among the islands prehistorically (Collins 1991, Vellanoweth 1998), and historical accounts indicate that nineteenth century ranchers occasionally moved foxes among the islands (Johnson DL 1975). Therefore, humans may have—until recently—reduced the genetic isolation of island foxes.

In the late 1990s, four populations of island fox declined catastrophically, which led to the federal listing of those subspecies as *endangered*. Each of these populations has rebounded following intensive management (Coonan et al. 2010), but the long-term effect of this population decline (two subspecies were reduced to 15 individuals) is unknown. Managers prioritized maintaining the island populations as distinct through this population crisis, in part to reduce the risk of parasite and pathogen transmission among populations but also because the federal listing mandated that each subspecies be recovered independently. When the fox populations are no longer listed, managers will need to decide how best to manage them over the longer term. An important consideration in that planning is the evidence of prehistoric and historic movement of foxes, which raises the possibility that, under current conservation management, the populations are more isolated than they have been for most of the last 10,000 years.

We also see traces of repeated isolation and evolution in the current distribution of the archipelago's flora. Of about 271 endemic plant taxa across the Channel Islands, 44 are single-island endemics (table 1), and 37 are shared only among the islands that once made up ancient Santarosae (Junak et al. 1997). Some endemic plants, such as island ironwood (*Lyonothamnus floribundus*), are Pleistocene relicts (Raven and Axelrod 1978/1995) that continue to thrive where isolated cool and moist insular microenvironments have persisted throughout the Holocene. The ancestors of other endemics radiated into open niches on the emerging islands, developing into novel types. The result is a flora uniquely tuned to the Channel Islands' present environments but with a distribution that reflects past dynamics.

The traits of many endemic plant taxa, however, are no longer adaptive in the altered conditions of the present. Simply removing grazing animals and allowing passive recovery may reverse the downward trajectories of some natives, but others will need additional help. Restoring the unique plants of the Channel Islands requires careful study of how habitat management—or strategic actions targeted at improving key demographic vital rates—can facilitate adaptation and viability. For example, recovery tools for the endangered plants of Santa Cruz Island include such activities as hand pollination to increase seed output, outplanting of new populations to buffer against microclimatic change, and invasive plant control to increase the survivorship of young recruits (McEachern and Wilken 2011). Planning is under way for a project on Santa Rosa Island to harvest fog drip in a restoration of upland chaparral to support several island endemic plants, which would simultaneously restore water recharge to the damaged ecosystem. On East Anacapa, a multiyear effort to replace nonnative figwort (*Malephora crocea*), planted by the US Coast Guard for erosion control in the 1940s, with natives is being rewarded by new finds of plants thought lost from the islet.

Channel Island vegetation communities provide habitat for many endemic animal taxa, making the interplay among historical baselines, vegetation management goals, and endemic species protection central to restoration planning. For example, loggerhead shrikes on the northern Channel Islands (*Lanius ludovicianus anthonyi*) have had limited gene flow with mainland populations for thousands of years (Caballero and Ashley 2011) and may be locally adapted to island environments or may be suffering from a loss of genetic variation due to small population size. Accounts of island shrikes from the early twentieth century described the populations as robust, even when the islands were extensively devegetated by overgrazing (see Collins 2008). Island loggerhead shrikes are now much more rare (Stanley et al. 2012). Causes for the shrike decline are under investigation, but habitat change is hypothesized to be an important factor. Shrikes thrive in a mosaic of patchy shrub cover, where woody plants afford perch sites for hunting in nearby open grass or bare ground. As woody plants recover, forming continuous and closed canopies and ever-larger patch sizes, shrike habitat quality decreases. The ideal balance of open ground and closed canopy for shrikes is unknown, which draws attention to the gap in knowledge about the condition of the vegetation on the islands during previous time periods (e.g., during the millennia of Chumash and Tongva occupation). Present-day land stewards will need to decide whether shrike habitat should be actively managed, recognizing that a focus on shrikes may involve trade-offs in other habitat and species recovery goals.

In addition to setting active population management policies on single islands, managers must also consider whether to establish new populations on others. For example, 19 endemic avian subspecies (of 14 species) are known to occur on one or more of the Channel Islands, and many (i.e., 10–13) of these taxa have been extirpated or have become threatened (Johnson NK 1972, Power 1994). Managers may decide to reestablish extirpated populations to restore ecological function. Extant populations that could serve as source populations, however, may exhibit local adaptation to the islands on which they currently reside. For example, prior to the 1960s, Channel Island song sparrows (*Melospiza melodia graminea*) showed strong interisland variation in bill size: larger-billed and more sexually dimorphic sparrows were found on the larger, warmer islands, with more continental climates (e.g., Santa Cruz, Santa Rosa, San Clemente), and smaller-billed, more monomorphic sparrows were on the smaller, cooler islands (e.g., San Miguel, Santa Barbara, Los Coronados off Baja California; Greenberg and Danner 2012). The sparrow populations were extirpated by the 1960s from three islands (Santa Barbara, San Clemente, and Los Coronados; Collins 2008). Knowledge of the adaptive differences between populations can help identify and match relevant selection pressures on potential reintroduction islands with the most suitable source populations. New genomic techniques and stable isotope analyses, in combination with careful field observations and experiments, will help characterize these adaptive differences (box 1; e.g., Newsome et al. 2010).

Reducing risks from climate change

Climate change has had a profound effect on the Channel Islands for millennia and creates ongoing challenges for the conservation of both natural and cultural resources. In setting restoration and conservation goals for species and natural communities on the islands, managers will need to anticipate how climate change may affect the likelihood of success of their management actions. Given the magnitude of ecosystem alteration in recent centuries and the anticipated pace of future climate change, managers may be confronted with stewarding novel ecosystems (Hobbs et al. 2009) and with making unprecedented management decisions.

Climate warming, alteration of precipitation patterns (Cayan et al. 2008), and potential changes in fog levels (LaDochy and Witiw 2012) may heighten the vulnerability of the archipelago's native species and communities. The environmental conditions to which species have adapted may shift, and habitats may change at a pace that exceeds the capacity of some species to adapt. Such effects might be especially problematic for island taxa with limited dispersal ability. We may already be seeing the effects of warming and changing fog patterns in the loss of mature reproductive individuals from some plant populations (Fischer et al. 2009) and high mortality in young plants from others (McEachern et al. 2009). For endemic annual plant taxa that germinate in response to particular patterns of precipitation and temperature, climate change may cause a failure to recruit and replenish the seed bank (Levine et al. 2008). Managers may need to consider unorthodox interventions, such as managed relocation (e.g., Morrison et al. 2011).

Many of the archipelago's plants and animals have persisted through Holocene environmental changes. However, some factors that have shielded these communities from environmental threats in the past may now contribute to

Box 1. Genomics and isotopes as tools for historical ecology.

Historical ecology integrates questions and methods from a variety of fields, including marine and terrestrial ecology, archaeology, history, geology, paleontology, and genetics. Genomics and stable isotope analysis have become important, complementary tools that can provide insight into the levels of genetic variation, changes in population size, species interactions, adaptation, and shifts in habitat and resource preferences through time in various taxa, including humans.

One of the most powerful applications of genomics to historical ecology is the use of ancient DNA to generate snapshots of genetic variability through time. Ancient DNA is genetic material from a nonliving source, including bone, teeth, seeds, feces (coprolites), skins, feathers, and fibers. Archaeological and paleontological materials and historical museum collections can contribute to ancient DNA studies. Although DNA from these materials is often degraded, new high-throughput sequencing and DNA capture technology enable the characterization of genetic variation at thousands of loci. Even with partial genomes, archaeogenomics—a rapidly growing field that produces large sequence data sets from archaeological material—can address important questions in historical ecology related to resource preferences, domestication, migration, population structure, and introduction or translocation events, which are particularly important on islands. These data can also offer useful information for restoring, rehabilitating, and managing novel island ecosystems.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analyses are commonly used by ecologists and archaeologists to quantify diet composition and variation. The isotopic composition of a consumer's tissues mirrors that of its diet but is offset by predictable amounts, such that $\delta^{13}C$ and $\delta^{15}N$ values increase by 1%–2% and 3%–4%, respectively, with each increase in trophic level. This approach can be used to study paleontological, archaeological, and historical material and to examine the effects of human influences on a species' dietary and habitat preferences.

Ongoing projects on the California Channel Islands are applying genomics and isotope analysis to a variety of bird and mammal species to better understand human impacts on island landscapes through time. For example, the endemic island fox (*Urocyon littoralis*) is an omnivorous apex predator of significant conservation concern. Despite decades of research, the origins of the island fox remain unclear, with researchers arguing for a natural, cultural (i.e., introduction by Native Americans), or combined dispersal of mainland gray foxes (which evolved into diminutive island foxes) to the six largest Channel Islands prior to 7000 years ago. Using ancient DNA, genomics, and isotopic analyses, researchers are weaving together a better picture of the origins and antiquity of the island fox and of the human–fox relationship through time. Genomic resources also have the potential to address the observed, potentially adaptive differences in body size, body shape, ecology, and behavior from mainland gray foxes. Isotope analyses of ancient, historical, and extant island fox populations are yielding information on foraging ecology, including the possibility of foxes' scavenging or sharing food with Native Americans. Together, these data will be useful in future management decisions for this endangered carnivore and represent an important integration of material and perspectives from a variety of disciplines.

future vulnerability. Isolation from the mainland has probably reduced colonization events, which has resulted in a depauperate flora and fauna with limited resistance to pathogens compared with their more genetically variable mainland counterparts. Geographic isolation seems to have protected Channel Island bird populations from outbreaks of the West Nile virus, which has repeatedly decimated mainland bird populations (Boyce et al. 2011), but climate change may lead to more-suitable conditions for pathogens, and the more limited genetic diversity of island birds may make them more vulnerable to such pathogens in the future. In the case of the Channel Islands, isolation can both shield island populations from exposure to introduced pathogens, predators, and herbivores over the short term and ultimately make island populations more vulnerable to such introductions.

Increased human visitation across the archipelago may also exacerbate exposure risks, especially on Catalina, the most heavily visited of the Channel Islands. As the human population grows in southern California, more people will visit the "Galápagos of North America." Increased human activity and drought frequency on the islands may lead to increased risks of wildfire ignition and spread (Duncan and King 2009) and to invasions of pests and pathogens, such as weeds, wood-boring insect pests (Coleman et al. 2011), and wildlife diseases (Coonan et al. 2010).

Sea level rise is a related threat that could imperil both natural and cultural resources along the California coast and may be particularly pronounced for islands around the world (Courchamp et al. 2014). Past sea level rise, particularly between about 15,000 and 12,000 years ago, when the rate of rise was most rapid (Peltier and Fairbanks 2006, Stanford et al. 2011), probably had important consequences for island flora and fauna by creating some habitats and eliminating others. For example, a rising sea produced an estuary near Abalone Rocks, on Santa Rosa Island, that persisted from at least 12,000 years ago to 6000 years ago and was home to a variety of estuarine shellfish that no longer occur around the islands (Rick et al. 2005). Terrestrial ecosystems throughout the northern archipelago became fragmented, which resulted in approximately 10,000 years of isolation of the sedentary terrestrial plant and animal populations, although humans may have moved some species (e.g., the island fox) among islands. Sea level rise also posed significant challenges for the first people that occupied the Channel Islands because of the reorganization of the island marine communities that were a primary source of human subsistence (Rick et al. 2005, Erlandson et al. 2011).

How will sea level rise affect the archipelago's plant and animal populations? To explore this question, we projected the effects of 5 meters of future sea level rise on the land area of the Channel Islands (see figure 3), a relatively high estimate, but one that is possible over the next few centuries (Jevrejeva et al. 2012). Because of the region's bathymetry and topography, this amount of rise will result in the loss of only about 1.4% of total island land area. Coastal erosion, which would likely accelerate over recent historical rates, could increase the area affected. Although this land area is small relative to that lost since the end of the Pleistocene, some coastal areas will probably be severely affected by sea cliff retreat, which would destroy cliff habitats for nesting birds and sea-bluff specialist plants and an untold number of archaeological sites. Coastal dune ecosystems, hotspots of biodiversity and endemism on the Channel Islands (Chatzimanolis et al. 2010), could be similarly degraded if sea level rise is too rapid for those habitat features to migrate inland or for organisms to adapt. Existing nearshore habitats, such as coastal dunes and freshwater marshes, could be lost, reduced, or relocated, which would directly affect the unique communities dependent on them, such as endemic dune insects, seabird nesting colonies, and populations of rare plants. Sea level rise is also predicted to alter or destroy northern elephant seal (*Mirounga angustisrostris*) rookery and haul-out sites on the mainland (Funayama et al. 2013) and will probably have similar impacts on large pinniped populations at Point Bennett, San Miguel Island, and elsewhere on the Channel Islands.

Seabirds, seals, and sea lions will probably adapt to such changes by seeking out new locations suitable for their needs, as they have done during previous periods of sea level rise. However, managers will need to carefully monitor the potential challenges that this reorganization poses to specific species. Managers will also need to decide whether to prioritize efforts to protect coastal dune and freshwater marsh habitats, a costly and challenging endeavor; to translocate dune-dwelling organisms with poor dispersal abilities from coastal sites to more inland sites; or to facilitate genetic exchange between increasingly isolated populations. Ultimately, the threat of sea level rise to both biological and cultural resources (e.g., the erosion of archaeological sites) emphasizes the need for conservation efforts in which both natural and cultural resources are considered and in which responses are quick to rapid changes. Coastal archaeological sites help reveal both the cultural history of the islands and their ecological and evolutionary history. The destruction of these sites as a result of sea level rise will result in a loss of knowledge about the past that may be important for ecosystem management in the future.

Conclusions

The populations, communities, and landscapes that constitute an ecosystem have a shared history. Many of the attributes that we currently observe and the potential responses of the future can be better understood through knowledge of that history. The flora and fauna of the Channel Islands share a Late Pleistocene and Holocene history of connectivity, separation, and climate change as sea levels have fallen and risen, with different effects on each island. These geologic processes influenced patterns of evolution and species turnover and provided the backdrop for 13,000 years of human interactions with the archipelago's wildlife communities.

Combining archaeological, ecological, historical, geological, climatic, and paleobiological data can illuminate the natural dynamism of ecosystems and can guide conservation decisions. In the Channel Island archipelago, the integration of such data sets within and across islands can fill gaps in knowledge and can provide greater power to detect patterns (Bakker et al. 2009). This approach is especially important in the Anthropocene, given the ecological novelty, risks, and uncertainties that will need to be managed. In the context of global change, experimentation and adaptive management will be increasingly important for conservation, and, consequently, so will coordinated research and management across the archipelago (e.g., Coonan et al. 2010). Fortunately, the archipelago can serve as an experimental arena, in which management actions on individual islands can be designed to test hypotheses and accelerate learning, so as to advance science and better inform conservation decisionmaking across the islands. For example, a management action to reintroduce an extirpated bird population could also be designed to examine the ecological and evolutionary mechanisms leading to variation in bill morphology among island birds (e.g., Greenberg and Danner 2012).

Although interdisciplinary science provides a necessary foundation for effective and efficient conservation management, it alone is insufficient to guide decisions. Science cannot decide whether the landscape or ecological processes of 2000, 200, or 20 years ago is the "ideal" management goal. Societal values frame these decisions. The Channel Islands represent a diversity of values, which manifest themselves through the public's and managers' mandates, missions, and actions. Recreation, for instance, is a common activity on most of the islands, but its character varies considerably across the islands. The removal of introduced vertebrate herbivores has been a management goal on all of the islands. Catalina Island, however, still has a large managed population (n = 150) of American bison (*Bison bison*), introduced in 1924 for the production of a movie, and mule deer (*Odocoileus hemionus*), introduced between 1928 and 1932 as a game species (Longhurst et al. 1952, Sweitzer et al. 2005, Duncan et al. 2013). Bison are a focal point of the visitor experience on Catalina, and the Catalina Island Conservancy administers deer hunting for the California Department of Fish and Wildlife. Do bison and mule deer belong on Catalina Island in the Anthropocene? Answers to such questions depend on the philosophical framework used as a basis for these decisions.

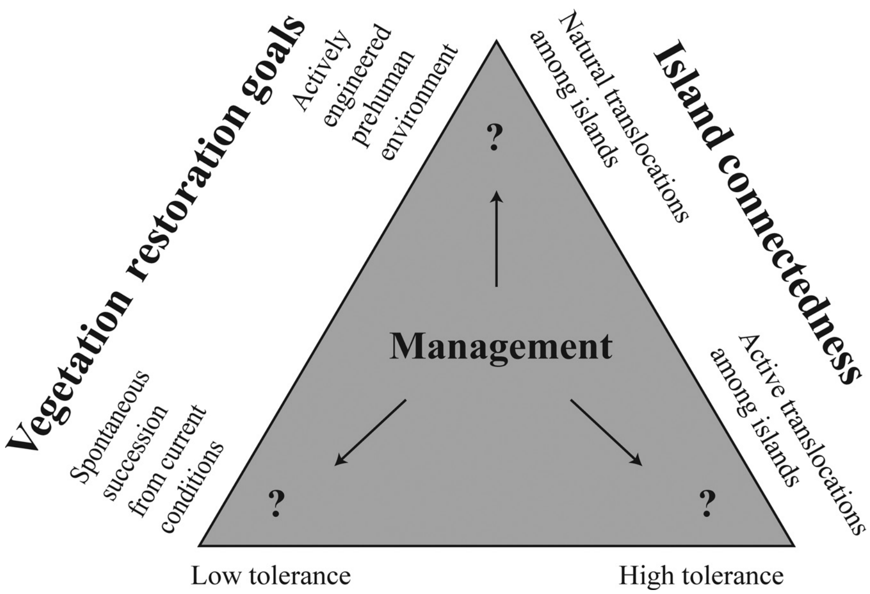

Figure 4. Tolerance level for human intervention and views on island connectedness can dramatically affect vegetation restoration goals and the scale of management plans.

Climate change will demand that managers make their conservation values explicit. For example, we expect to see changes—as we have in the past—in species composition on the islands as climates change and species ranges shift. Managers will need to decide which colonization events on an island will be considered natural (and acceptable) and which will merit an active management response, perhaps because of their potential ecological harm or because of their mode of arrival to the island (i.e., by intentional or accidental human introduction). Similarly, managers will need to decide which species declines to accept and which to actively resist. In some cases, managers may seek to actively facilitate interisland dispersal of island biota (Morrison et al. 2011); in others, they may seek to maintain isolation. As managers face the circumstances of natural or anthropogenic exchange of taxa across islands, knowledge of the prehistoric and modern connectivity and dispersal across islands can help guide conservation decisions. Extinction and colonization are processes that define island ecosystems (MacArthur and Wilson 1967). Managing this dynamism will require an understanding of the structure of natural communities and the interactions among species and of how human intervention has affected and would affect those relationships.

In the face of rapid environmental change, many island species and ecosystems will be effectively *conservation reliant* (*sensu* Scott et al. 2010), meaning that they will require attentive monitoring and a readiness to intervene to maintain their viability. Active management may be needed to establish most desired future conditions (figure 4). For example, careful monitoring to detect and manage introductions of alien invasive species will be an ongoing management imperative. One consideration in setting the desired future conditions for the islands will be identifying what types and degree of intervention are acceptable. A historical ecology perspective can guide such value systems and decisions, because the degree of past human influence—and its ongoing legacy—is better understood.

We raised two overarching questions at the beginning of this article, focused on the effectiveness of historical ecology in helping guide management and in providing baselines for establishing desired future conditions. Our analysis of three interrelated issues (setting restoration goals, preserving rare and endemic taxa, and reducing risk of climate change) helps answer these questions and shows how an interdisciplinary perspective on the long-term causes and consequences of environmental change can inform the management and conservation of the Channel Islands and other island systems worldwide. Long-term, interdisciplinary data provide baselines and elucidate targets to guide restoration (e.g., in Channel Island plant restoration). Although, in some cases, returning to past conditions may be impossible or undesirable, the past provides snapshots through time of ecosystems with and without humans under a range of climatic conditions that can frame appropriate future conditions. We have also shown how these island ecosystems are characterized by interactions between humans and wildlife that extend deep into the past. A fuller understanding of how humans have affected the ecology and evolution of the islands through time better prepares us to responsibly manage their ecology and evolution into the future. Although a historical approach does not answer all questions, the 20,000-year perspective presented here illustrates that human influence and global change have been fundamental drivers of Channel Island ecosystems for millennia. Using interdisciplinary data to understand this long-term change, as we are doing on the Channel Islands, provides an important model and strategy for enhancing conservation around the world.

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