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Ecosystem restoration on Santa Catalina Island: a review of potential approaches and the promise of bottom-up invader management

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ECOSYSTEM RESTORATION ON SANTA CATALINA ISLAND: A REVIEW OF POTENTIAL APPROACHES AND THE PROMISE OF BOTTOM-UP INVADER MANAGEMENT

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ABSTRACT.—Restoring large, complex landscapes can be challenging, especially given that some threats to native diversity and ecological function cannot be wholly eliminated. Santa Catalina Island, California, provides a valuable case study because its challenges include a variety of ecosystem threats, legal restrictions, and cultural attachments, as well as a vocal resident human population that often does not agree with conservation actions. Catalina Island has been highly modified by numerous invasive species, fragmentation and erosion from roads, altered hydrology from dams, and increased fire frequency. In this paper, I build on a previously published review of resources and threats and discuss potential management actions for those threats. Although the island's large size, rugged topography, and pervasive human influence limit management options, several feasible actions could have an important restorative effect. In particular, "bottom-up" invader management may be a relatively noncontroversial way to produce multiple positive outcomes. Reducing fragmentation, restoring natural hydrologic regimes, and augmenting native plant cover could disadvantage invasive plant and animal species while promoting the native flora and fauna.

RESUMEN.—El desafío de restaurar grandes y complejos paisajes puede ser difícil, especialmente porque algunas amenazas a la diversidad nativa y funciones ecológicas no pueden ser eliminadas por completo. La Isla Santa Catalina, California, proporciona un valioso caso de estudio, ya que cuenta con una variedad de amenazas al ecosistema, restricciones legales y añadidos culturales, así como una población humana residente que a menudo no está de acuerdo con las medidas de conservación. La Isla Catalina ha sido modificada por numerosas especies invasoras, la fragmentación y la erosión por los caminos, la hidrología alterada por las presas y un aumento en la frecuencia de incendios. En este artículo, construyo sobre un resumen previamente publicado de recursos y amenazas, y discuto las acciones potenciales de intervención para tales amenazas. Aunque el gran tamaño de la isla, la topografía escabrosa y la influencia humana limitan algunas opciones de intervención, varias acciones factibles podrían tener un efecto fortalecedor importante. En particular, el tratamiento "bottom up" (de abajo hacia arriba) del invasor podría ser una forma relativamente no controversial de producir múltiples resultados positivos. La reducción de la fragmentación, la restauración de los regímenes hidrológicos naturales y el aumento de la cobertura vegetal nativa podrían crear una desventaja para las especies de animales y de plantas invasoras, y promover la flora y fauna nativa.

Challenges of large-scale ecological restoration include technical issues such as ubiquitous and tenacious invasive species, institutional constraints such as funding and legal restrictions, and social challenges such as public resistance. Given these challenges, some threats to native species and ecoystems cannot be wholly eliminated. Santa Catalina Island, California, provides a case study of such land management challenges. The island has experienced a variety of anthropogenic stressors, including invasion by numerous transformative nonnative species, fragmentation and erosion from roads, altered hydrology from dams, and increasing fire frequency, which have left the ecosystem highly modified. The island's large size, rugged topography, and pervasive human influence reduce the likelihood that many transformer species can be eradicated. Thus, the island's land managers need to develop cost-effective, alternative means of reducing the adverse impacts of such species. A focus on species interactions, community dynamics, and ecosystem processes can be especially important for identifying those management alternatives (Zavaleta et al. 2001, Rayner et al. 2007).

Here, I discuss restoration alternatives for the major threats to Catalina Island's resources that were reviewed in Knapp (2010a), and I highlight how land managers might benefit from undertaking "bottom-up invader management" actions. Bottom-up invader management (*sensu* McEvoy and Coombs 1999)

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emphasizes the use of resource limitation to control invaders instead of top-down control methods, such as hunting. It may involve mitigation of stressors on native taxa, manipulation of disturbance regimes, soil conditions, and other abiotic factors, or increasing competition through actions such as seeding native plants (D'Antonio and Chambers 2006). Such activities on Catalina Island may also include dam and road removal, which are relatively noncontroversial actions that would not only ease the immediate stressors of hydrologic alteration, fragmentation, and denudation but would also have the secondary benefit of putting many of the island's plant and animal invaders at a disadvantage.

Setting and Management History

At 194 km^2, Catalina Island is the third largest of the 8 California Channel Islands and is located approximately 32 km from the southern California mainland coast (Schoenherr et al. 1999). The island is characterized by numerous steep canyons; perennial streams are limited to a few dominant canyons near the center of the island. The island has a long history of human use, from native Tongva settlements to Spanish missionaries, Yankee traders, and otter hunters in the early 1800s, and squatters, miners, and Union soldiers in the mid-1800s (Moore 2009). Between the mid-1800s and mid-1900s, multiple ungulates were introduced, including feral goats (*Capra hircus*), feral pigs (*Sus scrofa*), American bison (*Bison bison*), mule deer (*Odocoileus hemionus californicus*), domestic sheep (*Ovis aries*), and cattle (*Bos taurus*), resulting in the deterioration of habitat (Coblentz 1980). Sheep and cattle were the first nonnative animals to be eliminated on the island by the mid-1920s and late 1950s, respectively (O'Malley 1994). Cumulatively, browsers have reduced the extent of shrubland on the island, which has been replaced with introduced annual grasses (Minnich 1982). Introduced ungulates have also caused the open understory of much of the island's oak stands. The consequent reduction of vegetation structure and diversity has undoubtedly reduced the abundance and diversity of the wildlife that depend on it, from invertebrates (Lawton 1983, Bennett 1993) to native vertebrates (Tietje and Vreeland 1997, Sillett et al. 2012).

Catalina Island is the only one of the 8 California Channel Islands with an incorporated city (Avalon), and the island receives about one million visitors per year (Catalina Island Chamber of Commerce and Visitors Bureau 2012), the majority of whom remain in Avalon. The founding of Avalon led to increased development of the rest of the island, including a stagecoach route and hunting lodge; a World War II camp; ranch settlements, dams, and camps in the majority of the island's coves; and an airport carved off of one of the tallest peaks on the island. Today, the Catalina Island Conservancy (hereafter, Conservancy) owns and manages 88% of the island; its mission is to be a responsible steward of the land through a balance of conservation, education, and recreation.

The Conservancy has taken important steps to recover the island from centuries of human impacts. Feral goats and pigs have been removed, a hunting program is maintained for mule deer, and bison are managed through a contraception program. The most transformative nonnative plant species have been identified, and they are being managed throughout the island by focusing simultaneously on eradication of limited-abundance, high-impact species and control of more widespread species in priority areas (Knapp 2010b, Knapp et al. 2011). The Catalina Island fox (*Urocyon littoralis catalinae*) has been brought back from the brink of extinction, following an outbreak of canine distemper virus, through a combination of translocations, captive breeding, and vaccinations (Coonan et al. 2010). Yet much more remains to be done to ensure the persistence of at least 42 taxa found only on Catalina Island (as well as a number of other Channel Island endemic taxa) and to maintain diverse, resilient communities. Herein I review management alternatives for threats stemming from invasive species and habitat alteration and discuss how managing the latter may be a means to help manage the former.

Threat Management Options and Feasibility

Mule Deer

The impacts of introduced deer species are especially severe on islands, where deer lower species richness, change community composition, endanger rare plants, and reduce wildlife populations of various trophic levels (reviewed in Knapp 2010a). On Catalina Island, mule deer reduce shrub and tree cover and survivorship, particularly postfire (reviewed in Knapp 2010a). In contrast to many of the other invasive wildlife species on the island, mule deer eradication on Catalina Island is technically feasible, as evidenced by the prior removal of both feral goats and feral pigs (Schuyler et al. 2002a, 2002b), the recent removal of deer and elk (*Cervus elaphus*) on nearby Santa Rosa Island (Kettmann 2011), and improvements in the technology available to detect and dispatch ungulates, thus ensuring their complete removal (Morrison et al. 2007). An increase in native perennial grasses and shrubs, as well as a decrease in exotic annual grasses, was found on Santa Rosa Island following removal of cattle and reduction of both Roosevelt elk and mule deer herds, although effects vary by taxa, functional group, and physical environment (Christian et al. 2008, Corry and McEachern 2008, Dow et al. 2008).

Mule deer eradication would require either permission from the California Department of Fish and Game, which has legal jurisdiction over the deer, or a change in state law. The Conservancy has sought permission for private control over management efforts with little success to date. A change in state regulation would likely be required. Mule deer have been harvested almost annually on the island from 1949 through the present, most recently as part of the Private Lands Management Program of the California Department of Fish and Game. However, recreational hunting alone is unlikely to sufficiently control an invasive mammal such as mule deer (Mack et al. 2000).

American Bison

American bison reduce plant diversity and cover on Catalina Island, simplify habitat structure, trample woody species such as oak trees, and facilitate the dispersal of nonnative plants. However, they also appear to have the beneficial effect of controlling invasive annual grass densities (reviewed in Knapp 2010a). Bison are currently managed to approximately 150–200 individuals on roughly one-half of the island via immunocontraception (Duncan et al. 2013). Their complete removal would be technically feasible, given prior success of roundup efforts on the island and removal of ungulates on multiple other islands. There would be social obstacles, however, as the bison are a beloved feature of the Catalina Island landscape and a source of ecotourism dollars. Restriction of their range to a location most visible to tourists could be a viable solution and is the option favored by research scientists (Sweitzer et al. 2003). Restricting bison presence to the most heavily toured area of the island would balance maintenance of the ecological integrity of the island with cultural and economic considerations.

Cats and Rats

Cats (*Felis catus*) and rats (*Rattus* spp.) are believed to be responsible for the extinction of hundreds of taxa, including birds, small mammals, herpetofauna, and invertebrates (reviewed in Knapp 2010a). In addition, rats can restrict plant regeneration and abundance, and cats are believed to compete with the Catalina Island fox (reviewed in Knapp 2010a). The ecological effects of these 2 species on Catalina Island are not well understood, however, and it is possible that the presence of a native predator, the fox, moderates feral cat impacts (McChesney and Tershy 1998).

Management of introduced cats and rats on Catalina Island is complicated by their combined presence, as well as the presence of multiple nontarget species, such as native rodents, birds, and foxes. Removal of cats without control of introduced rats could have the unintended consequence of reducing native wildlife populations even further through mesopredator release (Courchamp et al. 1999, Rayner et al. 2007). Fan et al. (2005) recommend controlling the rodents first and the cats second, or controlling both simultaneously. Although eradication of rodents first may further increase predation by cats on threatened native species (Courchamp et al. 1999), the benefits of eventual removal of the superpredator may outweigh the immediate costs of mesopredator release (Russell et al. 2009).

Transformer rodents such as rats have been eradicated from 284 islands, the largest of which is 11,300 hectares (Howald et al. 2007). Aerially applied rodenticide is used in the majority of those eradications (Howald et al. 2007), and captive management or translocation of native species in danger of nontarget poisoning can reduce impacts to those species (e.g., Shah 2001, Merton et al. 2002, Howald et al. 2005). Feral cats have been removed from at least 48 islands globally, the largest of which is Marion Island, at 290 km^2, or 71,660 acres (reviewed in Nogales et al. 2004). However, that removal was accomplished only with 19 years of sustained effort and multiple methods on an island with no permanent human population (Bester et al. 2002). This long-term commitment and lack of public opposition was undoubtedly critical to that project's success. Cats were recently removed on San Nicolas Island, California, primarily through live capture (Hanson et al. 2010, Stephenson-Pino 2012). However, the modified padded leghold traps used on that project are only legal on federally owned lands in California (Hanson et al. 2010).

The eradication of both cats and rats on the entire Catalina Island would be hindered by the presence of vocal opponents, the existence of extensive cat colonies on public land, the large size and ruggedness of the island, and the presence of nontarget native species. Localized control in priority areas could be a viable management alternative to eradication (Jouventin et al. 2003, Ogden and Gilbert 2009); however, long-term efforts can be prohibitively costly (Howald et al. 2005) and toxin buildup in the environment or evolution of toxin resistance is a concern (Innes and Barker 1999). Rat-proof exclosures, such as those described by Campbell and Atkinson (2002) or Day and MacGibbon (2007), have been used successfully and can minimize the need for ongoing control. They are being used to protect areas up to 250 ha in New Zealand (McLennon 2006) and could conceivably be altered to exclude cats as well.

Habitat restoration could limit the impacts of invasive rats. In Madagascar, rats were more abundant in smaller habitat fragments, while endemic rodents declined in such fragments (Ganzhorn 2003). Unnecessary roads could be removed and revegetated in order to provide the contiguous habitat that favors native species over these invaders. Additionally, immunocontraception, including that vectored by species-specific viruses, may be a promising technique (Courchamp et al. 2003, Hardy et al. 2006).

European Starlings

European Starlings (*Sturnus vulgaris*) have negative effects on other members of the woodpecker family, as well as on some birds in other families (reviewed in Knapp 2010a). They also preferentially disperse seed of nonnative plant species over natives (reviewed in Knapp 2010a). Due to the starling's status as an agricultural pest, much effort and funding has been expended on its deterrence and control (e.g., Garner 1978). Harassment using both visual and sonic frightening devices has been utilized in the United States, but with little success (Brough 1969, Clark 1976, Garner 1978, Belant et al. 1998, Seamans et al. 2001, Blackwell et al. 2002). Such deterrents are not successful in the long term and only move the problem elsewhere (Feare et al. 1981, Dinetti 2006). Several methods of lethal control have been used, including application of a chemical avian stressing agent (Starlicide), dynamiting, and shooting (Clark 1976, Garner 1978, Feare 1991). The avian stressing agent reduced the starling population to varying degrees, from <1% to 99% (Garner 1978). Killing programs for bird pests are expensive and generally unsuccessful, due to both immigration from neighboring areas and compensatory reproduction (Feare 1991). Furthermore, some of the methods are particularly inhumane.

The most promising avenue for starling control is through habitat management. Generally, starlings favor disturbed, homogeneous habitat (such as agricultural fields or invaded monocultures); therefore, their concentrations could be limited by enhancing native habitat cover and heterogeneity (Clergeau and Fourcy 2005). One component of this approach may be herbivore removal. Diamond and Veitch (1981) have reported that browsers and grazers are a factor in bird invasion, along with habitat fragmentation.

Wild Turkeys

It is not known if Wild Turkeys (*Meleagris gallopavo*) still occur on Catalina Island. However, if they do still exist, they are expected to have negative effects on plant regeneration, particularly oaks (reviewed in Knapp 2010a). Under the precautionary principle, land managers have eradicated Wild Turkeys from Santa Cruz Island (Morrison 2007). Wild turkey removal on Catalina would be relatively feasible, given their limited distribution and large size.

Brown-headed Cowbirds

Brown-headed Cowbirds (*Molothrus ater*) are brood parasites and may have a substantial adverse effect on rare passerine bird populations (reviewed in Knapp 2010a). Like the

European Starling, the Brown-headed Cowbird is favored by human-modified habitats and fragments (Lowther 1993). Trapping at important breeding areas has been the only means of successful control of Brown-headed Cowbirds to date (Lowther 1993). Research conducted by Staab and Morrison (1999) suggests that riparian management favoring greater understory cover can help to reduce parasitism by this species. This objective could be promoted by ungulate removal and habitat restoration, as with starlings.

American Bullfrogs

American bullfrogs (*Rana catesbeiana*) are believed to be at least partly responsible for the decline or extinction of 7 native frogs in the Southwest, along with many other native amphibians elsewhere in the world. They pose a risk to snake and fish populations (reviewed in Knapp 2010a), and they have also been the causal agents of diseases such as chytridiomycosis, which is implicated in global amphibian declines (reviewed in Knapp 2010a). No island-specific data have been collected regarding their impacts, but bullfrogs occupy reservoirs throughout the island.

It is widely agreed that bullfrogs are extremely difficult to eradicate due to their high fecundity, density dependence, and evasiveness (Schwalbe and Rosen 1988, Lever 2003, Adams and Pearl 2007). Eradication and control methods used to date include electrification of pond water followed by manual removal of both adults and larvae; chemical and biological control methods; funnel traps; lethal control with air rifles or gigs; and the clearing of vegetation and addition of lime to eliminate eggs and tadpoles (Schwalbe and Rosen 1988, Lever 2003). However, population reductions have been small and short-lived, even in relatively isolated desert ponds (Schwalbe and Rosen 1988). Results of bullfrog population models suggest that they may be most effectively controlled by culling juvenile frogs in the fall (Govindarajulu et al. 2005) or with a combination of lethal control of adults and pond draining at least every 2 years (Doubledee et al. 2003). However, a combination of adult capture, pond drainage, pond excavation, and capping did not fully eradicate the frogs in one British pond, presumably because frogs are able to remain deep in burrows and vegetation (Lever 2003).

The best prospects for invasive bullfrog control appear to be habitat management (Adams and Pearl 2007). Because bullfrogs overwinter as larvae (tadpoles) in the water, they generally cannot live in water sources that frequently dry up (Orchard 1999, Maret et al. 2006). The Conservancy could actively manage ponds and reservoirs on the island to favor native wildlife by promoting more ephemeral wetland habitats over permanent ponds (Adams 1999, 2000, Maret et al. 2006) and by encouraging shallow water, sloping banks, and emergent vegetation (Kiesecker et al. 2001, Porej and Hetherington 2005, Adams and Pearl 2007, Minowa et al. 2008). Dam removal would facilitate these goals.

European Honey Bees

The balance of evidence suggests that European honey bees (*Apis mellifera*) have a negative impact on native bees and that they reduce pollination services, decrease the seed set of native plants, and preferentially pollinate the flowers of nonnative plants (reviewed in Knapp 2010a). Oldroyd (1998) reviewed the known methods for controlling honey bees, which include manual hive location or pheromone lures and insecticide application or remote application of insecticide through trained forager bees. Honey bees have been declining in North America due to a combination of pesticides, parasitic mites, and invasion of the African honey bee (Sugden et al. 1996); and such natural stressors have been used to the advantage of honey bee management on Santa Cruz Island (Wenner et al. 2000). Prior to this action, honey bee colonies were identified by their foraging patterns and ranges (Wenner and Thorp 1994) then removed by closing off all entrances to the colony, inducing suffocation (after anesthetization; Wenner et al. 2000). Swarm traps baited with pheromones were also used to attract the bees (Wenner et al. 2000).

Habitat restoration could also be practiced to moderate the effects of introduced honey bees. Ongoing removal of transformer plants used by honey bees, such as fennel (*Foeniculum vulgare*), yellow star-thistle (*Centaurea solstitialis*), and flax-leaf broom (*Genista linifolia*), would remove any facilitation between these invasive species. In addition, native nectar- and pollen-producing plants could be supplemented, particularly those that will increase diversity, to ensure that floral resources are not limiting for native species (e.g., Paton 2001) and to increase native bee diversity (Hopwood 2008). Lastly, habitat clearing and fragmentation could be minimized, as this favors honey bees (Aizen and Feinsinger 1994), and all island landowners could adopt a policy that prohibits managed honey bee hives.

Argentine Ants

Argentine ants (*Linepithema humile*) are associated with reduced arthropod diversity and abundance and native bee foraging, as well as the disruption of mutualistic and parasitic relationships (reviewed in Knapp 2010a). The presence of ants can shift entire food webs and may also impact small mammals, birds, reptiles, and amphibians (reviewed in Knapp 2010a). On Catalina Island, Argentine ants are associated with reduced native ant diversity, particularly of endemic species (Backlin et al. 2005). There is a large amount of literature on chemical control methods for Argentine ants, particularly in urban settings and agricultural areas (reviewed in Rust et al. 2003, Soeprono and Rust 2004, Klotz et al. 2007). Some eradication attempts have recently been successful for a variety of invasive ants on islands, including the Argentine ant (reviewed in Silverman and Brightwell 2008). Factors that have contributed to the success of these efforts have been the presence of only small, localized infestations; the use of a helicopter to spread bait; and a combination of techniques, including the removal of alternative food sources (Silverman and Brightwell 2008). A combination of synthetic trail pheromones and insecticide can also be effective (Sunamura et al. 2011). Recently, an experimental bait distributed in hydrated polyacrylamide beads has been applied in a trial area on Santa Cruz Island with great success and minimal disturbance (Boser et al. 2014a), and this bait is currently being applied to other locations on the island via helicopter.

A variety of techniques other than chemical means could be investigated to limit Argentine ant abundance. Promoting increased aggression within Argentine ant supercolonies by adding individuals of different genotypes may reduce densities of this social species (Suarez et al. 1999, although see Tsutsui et al. 2003, Buczkowski and Silverman 2006, and Thomas et al. 2006). Alternative approaches to pesticides include the use of disruptive hormones and pheromones (Krushelnycky et al. 2002, Suckling et al. 2008). Biological control may also be successful, if an appropriate natural enemy can be identified (Silverman and Brightwell 2008). Lastly, bottom-up approaches could help favor native taxa over Argentine ants. Because fragmentation of natural habitat increases the success of Argentine ants, maintenance of unfragmented habitat blocks is particularly important to invasion resistance (Bolger 2007), as is limiting urban runoff and irrigation (Menke and Holway 2006).

Invasive Plants

The Conservancy has supported extensive management of transformer plants. This has involved a thorough mapping of all manageable invaders then eradication of high-impact, low-abundance species and control of high-impact, high-abundance taxa in priority areas (Knapp and Knapp 2005, Knapp 2010b). Treatment along dispersal corridors and prevention of new introductions are integral components of this effort (Knapp 2010b). In areas of extensive invasion, control could be combined with revegetation efforts to ensure that these areas are not colonized by undesirable species. Integrated vegetation management, which combines invasive plant control with native outplantings and manipulation of biotic and abiotic factors that control plant establishment and growth, can be effective (Sheley and Krueger-Mangold 2003, D'Antonio et al. 2004, Erskine-Ogden and Rejmánek 2005).

Nonnative annual grasses are not currently addressed in the Conservancy's invasive plant management program because they are ubiquitous throughout the island and consequently difficult to manage. These grasses—including bromes (*Bromus* spp.), wild oats (*Avena* spp.), ryegrass (*Lolium* spp.), barley (*Hordeum* spp.), Arabian or Mediterranean grass (*Schismus* spp.), and fescue (*Vulpia* spp.)—have many deleterious impacts. They hinder woody plant regeneration; suppress the growth of native shrubs, forbs, and perennial grasses; shift nutrient cycling regimes; change hydrologic and geomorphic processes; reduce forage quality for small mammals; facilitate insect pests and diseases; and promote increased fire frequency (reviewed in Knapp 2010a).

Invasive annual grasses cannot be eradicated from the island, but localized control can be accomplished with some effort. A diversity of species and functional groups will enhance establishment, persistence, and resistance to invasion (Levine 2000, Pokorny et al. 2005, Sheley and Half 2006). In particular, early-season forbs would best match the phenology of the annual grasses and potentially limit their abundance (Cleland et al. 2013).

Roads

Roads can impact ecosystem function and biodiversity by increasing runoff, erosion, and stream sedimentation; altering stream flow and duration; reducing and altering habitat; increasing wildlife disturbance and mortality; promoting invasion of exotic plants and animals; increasing pollution; promoting fire ignition; and forming a barrier to dispersal for smaller species, such as invertebrates, amphibians, and reptiles (reviewed in Knapp 2010a). The fragmentation caused by roads creates extensive stretches of edge habitat that favor invasive wildlife species, such as rats, starlings, Argentine ants, and honey bees (reviewed in Knapp 2010a). Vehicles were the predominant source of island fox mortalities during a recovery program for the endangered species (Carlos de la Rosa, Catalina Island Conservancy, personal communication).

Two actions that would minimize the effects of roads on Catalina Island are (1) removing some roads and (2) posting and enforcing maximum speed laws. Road removal is used more and more frequently as a restoration technique (Havlick 2002), but few published research studies exist on this technique (Switalski et al. 2004). However, a number of road reclamation handbooks exist (e.g., wildlandscpr.org). Road restoration typically involves decompacting, or "ripping," the road surface and recontouring hillslopes (Switalski et al. 2004). Recontouring can accelerate recovery, while simply abandoning a road does not recover belowground properties (Lloyd et al. 2013). Soil amendments may be added to increase nutrient cycling, and then the area is revegetated (Switalski et al. 2004). Silt fences, check dams, and other erosion control structures are used to reduce erosion and landslide risk (Switalski et al. 2004).

Water Impoundments

Water impoundments artificially homogenize water flow regimes, decrease valuable sediment loads downstream, and alter water tables, water temperatures, and stream channel morphology (reviewed in Knapp 2010a). The ecological consequences of these effects can include reduced cover, connectivity, and diversity of riparian vegetation; facilitation of exotic species such as bullfrogs, tamarisk (*Tamarix* spp.), and predatory fish; and alteration of entire food webs (reviewed in Knapp 2010a). While these impacts have predominantly been determined in larger river systems than those on Catalina Island, even a portion of these impacts would be cause for concern. The majority of Catalina Island's watercourses have water impoundments (a total of 27 impoundments exist: 2 are concrete dams, the remainder are earthen), and some have several.

Water impoundment removal has become more common worldwide over the past 2 decades in an attempt to restore river and stream processes (e.g., Hansen and Hayes 2012, Kil and Bae 2012, Renofalt et al. 2013). Reestablishing natural hydrologic processes aids in invasive species control and restoration in desert river and riparian oak ecosystems (Stromberg and Chew 2003, Bossard and Randall 2007). Due to an initial increase in sedimentation downstream, macroinvertebrate richness and densities may actually be reduced following dam removal (Chiu et al. 2013, Renofalt et al. 2013). However, this undesirable response diminishes with time, and complete recovery to preimpound states can be achieved after several decades (Hansen and Hayes 2012, Chiu et al. 2013). In addition, the abundance of nonnative invertebrate taxa may be reduced, which could have positive food web effects (Cross et al. 2011). Unassisted recovery rates can vary by proximity to source populations of native taxa. For example, benthic invertebrates may only recover when the source populations of desired taxa are found within 5 km of the restoration site (Sundermann et al. 2011).

Fire

Fire is a natural disturbance in Mediterranean-type ecosystems; however, high fire frequency can eliminate woody plants and cause a type conversion to nonnative annual grassland (reviewed in Knapp 2010a). Fire size has been increasing on Catalina Island over the last century, and the fire season has been expanded (Catalina Island Conservancy, unpublished data). Given that fires are exceedingly difficult to prevent and control, the only ways to limit the recurring frequency of fire on the island are to minimize ignitions to the extent possible and continue to manage burns as they occur. Strategies could include limiting human use of high-risk areas and conducting prefire planning (Keeley 2002).

Although a draft fire management plan has been produced ("Firewise 2000" 2003), it advocated prescription burning as a means for preventing large wildfires. This type of mosaic rotational burning may not be appropriate for the habitat types and conditions on Catalina Island (Moritz 2003, Keeley and Zedler 2009). In addition, slope stability is of concern following a burn (Keeley 2004). Rotational burning may also degrade shrublands by increasing the fire frequency (Zedler and Seiger 2000, Keeley 2002). An updated, ecologically sound fire management plan is necessary, and it should identify wildland areas that have recently burned or in which a new burn would have particularly detrimental effects, as well as potential defense locations and preferred burn perimeters. The plan could be used by island firefighters and the Conservancy to quickly identify priority areas for wildland fire control in the event of an ignition. To be effective, however, the plan must be adopted by island fire officials and updated regularly.

DISCUSSION

While there are many constraints to ecosystem restoration on Catalina Island (not the least of which are high human visitation and public opposition to control of some invasive animals), this review highlights a number of opportunities as well, with a potential myriad of cascading positive effects. Removing and revegetating selected roads would not only reduce fragmentation, erosion and stream sedimentation, road kill, pollution, and fire ignition, it may also disadvantage invaders such as rats, Argentine ants, honey bees, starlings, and Brown-headed Cowbirds in those areas. Similarly, restoring natural stream flow regimes by removing dams and revegetating waterways would not only enhance riparian and oak woodlands but would also put invasive bullfrogs and tamarisk at a disadvantage. In both cases, native wildlife species would be provided the maximum natural resources possible and given the best chance of successfully competing with or evading predation by invasive animals, such as cats, that cannot be otherwise managed. This concept has been called "bottom-up invader management" (D'Antonio and Chambers 2006) and is an appealing alternative on a degraded island such as Catalina Island where eradication of some transformative invasive species is unlikely.

Mule deer have a strong negative impact on the island's biota; their eradication would be technically feasible but would require a change in state law. Bison have similar negative effects on woody plant species but may also have the positive effect of controlling exotic annual grasses and are an important ecotourism attraction. Perhaps deer removal would reduce the pressure on woody plant species enough that the effects of bison would be less critical. Deer removal would have the additional benefit of recovering plant cover and structural diversity, which would further decrease the disturbance and fragmentation that favors other invaders, both plant and animal.

For most other invaders, including cats, rats, bullfrogs, starlings, cowbirds, and Argentine ants, successful eradication is unlikely for both logistical and social reasons. Bottom-up invader management might be the best way to disadvantage those species and, equally important, to support healthy populations of native wildlife that are better able to withstand their effects. As an example, ground squirrels may be depredated by feral cats. However, ground squirrel populations are more limited by bottom-up factors, such as burrow site availability and food plant abundance (Van Horne 2007), than by the presence of predators (Byrom et al. 2000). Increasing the amount of food and habitat available to the squirrels may counter some population effects of predation by feral cats.

In contrast to these other species, European honey bees could feasibly be eradicated, as has been accomplished on nearby Santa Cruz Island. Island-specific data regarding their impacts and ecological interactions, as well as their distributions, would help to both justify and prepare for such an undertaking. Even if impacts have not been determined, eradication of potentially harmful introduced species can be justified under what is called the "precautionary principle" (IUCN 2000, Clergeau et al. 2004, Hulme 2006). This same reasoning could be applied to the eradication of the wild turkey.

Continued diligence is important to ensure the long-term success of the Conservancy's invasive plant management program, as aboveground populations are eliminated but seed banks remain. Maintaining such commitment when the problem is visually reduced is one of the main challenges to successful plant eradication (Mack and Lonsdale 2002). Periodic remapping should be undertaken to accomplish early detection of and rapid response to new invaders and reemerging species from seed banks. Aerial surveys are a powerful, low-impact tool for detecting small populations of new invaders (Mack et al. 2000). Helicopter transport can also be used very effectively to remove remote infestations of transformer plants (Knapp et al. 2011). Further, expanded invasive plant control combined with native outplantings would not only benefit native biodiversity but may also disfavor European honey bees.

The order of any management actions undertaken by the Conservancy should take into account cascading trophic effects and the need for access in order to avoid unintended consequences (Zavaleta et al. 2001, Morrison 2011). As a hypothetical example, if cats and rats were to be excluded from a limited area, this should happen first while the vegetation is degraded and open and trapping is more feasible. Dam removal and mule deer eradication would initiate substantial vegetation recovery and should logically occur after removal of cats and rats. Lastly, selected roads should be removed only when this access is no longer needed.

Considering the high risk of additional future introductions and the complexity of eradication and control programs, prevention should be one of the highest priorities for future conservation efforts on Catalina. It is widely agreed that the most desirable scenario is to prevent species introductions before they occur (e.g., IUCN 2000, Rejmánek and Pitcairn 2002, Courchamp et al. 2003); therefore, biosecurity measures are needed (e.g., Boser et al. 2014b). Even species that are already present, such as rats, could either introduce deadly new pathogens or gain the genetic variation necessary to become more successful (Suarez and Tsutsui 2008). Catalina Island is no stranger to the risks of introduced pathogens, as the island fox population declined by 95% after exposure to canine distemper virus (Timm et al. 2009).

Extensive education and outreach efforts are needed to obtain the community support that is critical to the success of invasive species prevention, eradication, and control programs (IUCN 2000, Morrison et al. 2011). Legal action may sometimes be required (Myers et al. 1998). Although conservation efforts on Catalina Island are constrained by many factors, some of those same constraints are also key assets. The high level of visitation to Catalina makes it an ideal educational and outreach center for the southern Channel Islands. The Conservancy's Nature Center and Botanical Garden provides a venue for outreach regarding the uniqueness of the islands, the threats that face them, and the benefits of restoration. The island's residents also gain from the Conservancy's conservation actions in the form of ecotourism dollars (Wilson 2000).

In conclusion, although ecosystem restoration of Catalina Island will not be quick, cheap, or easy, the potential returns in ecological resilience may be substantial. Given real logistical and social constraints on some restoration options, the managers of Santa Catalina Island might best pursue options that will enhance this resilience from the bottom up. By restoring natural hydrologic processes and habitat connectivity, native species would be favored over invaders that benefit from fragmentation, altered disturbance regimes, and reduced biodiversity. Combined with expanded efforts to educate the public about these threats and to prevent future nonnative species introductions, the island could be a model for management of altered ecosystems.

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