

Responding to Ecosystem Transformation: Resist, Accept, or Direct?

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Before and after photos of a coral bleaching event in American Samoa. Photo credit: The Ocean Agency/XL Catlin Seaview Survey.

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DOI: 10.1002/fsh.10506

Ecosystem transformation can be defined as the emergence of a self-organizing, self-sustaining, ecological or social–ecological system that deviates from prior ecosystem structure and function. These transformations are occurring across the globe; consequently, a static view of ecosystem processes is likely no longer sufficient for managing fish, wildlife, and other species. We present a framework that encompasses three strategies for fish and wildlife managers dealing with ecosystems vulnerable to transformation. Specifically, managers can *resist* change and strive to maintain existing ecosystem composition, structure, and function; *accept* transformation when it is not feasible to resist change or when changes are deemed socially acceptable; or *direct* change to a future ecosystem configuration that would yield desirable outcomes. Choice of a particular option likely hinges on anticipating future change, while also acknowledging that temporal and spatial scales, recent history and current state of the system, and magnitude of change can factor into the decision. This suite of management strategies can be implemented using a structured approach of learning and adapting as ecosystems change.

INTRODUCTION

Changes in ecosystem composition, structure, and function are increasing in frequency across the globe (Pörtner et al. 2014; Settele et al. 2014; Whitmee et al. 2015; Nolan et al. 2018). Here, we refer to a subset of these changes as ecosystem transformations, which we define as emergence of a new ecosystem (i.e., a self-organizing, self-sustaining, social–ecological system) that deviates from prior ecosystem composition, structure, and function. The rate, magnitude, and areal extent of ecosystem changes now occurring, as well as high uncertainty about future system trajectories, pose critical challenges for fisheries and wildlife management. In a rapidly changing environment, a static view of ecosystem structure and function is insufficient. Instead, a dynamic approach is needed that explicitly considers the emerging reality that ecosystems may stray, gradually or suddenly, from historical conditions.

Ecosystem change has long been a primary focus of ecology (Odum 1953). Various conceptual models to describe ecosystem dynamics have emerged that are useful for understanding and managing ecosystem changes. Classical theory and empirical studies of succession are typically described as predictable and directional changes in community composition occurring over timescales ranging from decades to centuries that eventually lead to a “climax” or stable state (Cowles 1901; Shelford 1911; Clements 1936; Pickett et al. 2009). This view has been challenged by paleo-ecological studies that reveal how modern ecosystem states are only stationary over short timescales (e.g., years to decades; Davis 1981; Webb 1981; Jackson et al. 2009; Jackson and Blois 2015). In addition, ecologists now recognize the possibility of alternative stable states (Lewontin 1969) in which ecosystems may exhibit multiple stable configurations, despite similar environmental conditions because of historical, possibly idiosyncratic, states (i.e., hysteresis; Scheffer et al. 2001; Beisner et al. 2003). When environmental conditions exceed threshold values, a current stable state may undergo drastic, persistent, and nonlinear state-shifts (i.e., critical transitions) in ecosystem configuration (Holling 1973; May 1977; Scheffer et al. 2001; Beisner et al. 2003; Keeley et al. 2019). Other, recent definitions of ecosystem change that describe critical transitions in system dynamics include phase shifts and regime shifts (Folke et al. 2004; Petraitis and Dudgeon 2004; Vert-pre et al. 2013) or ecosystem collapse (Keith et al. 2013). Finally, many models that describe causes of ecosystem change exist (e.g., trophic cascades; Carpenter et al. 1985). Here, we view ecosystem transformation as a general dynamic encompassing gradual or rapid changes from a current state to an alternative persistent state. Such transformative change can sometimes result in novel system configurations that lack historical analogs at the current place (Williams and Jackson 2007; Hobbs et al. 2009, 2014). Although multiple transitions may occur as a result of certain drivers, they may not always bring about a new stable state (e.g., Hobbs et al. 2012).

Ecosystem transformation may be an inevitable outcome of the combined impacts of multiple drivers, including expanding human activities and rapid contemporary climate change. Climate is the most fundamental determinant of ecosystem state and function (Whittaker 1975; Peters et al. 2008; Pettoirelli 2012; Biggs et al. 2018). The range of climatic variables at daily, seasonal, and interannual scales are strong predictors of many biomes, individual species, community structure, and ecosystem processes at coarse spatial resolutions. A number of human activities, including pollution, natural resource extraction, land use, species translocations, and food and energy consumption impose stresses on ecological systems, often leading to drastic changes (Diaz et al. 2019).

Ecosystem transformation is not a new phenomenon when ecosystems are viewed through a paleontological perspective. Climate change has driven transformations for millions of years, and few contemporary terrestrial ecosystems are more than a few thousand years old (Jackson 2012; Nolan et al. 2018). Ecosystems have been altered by human activities at least since human use of fire, and those alterations have continued with development of agricultural and industrial societies; both marine and terrestrial ecosystem states have transformed dramatically over centuries to millennia (Jackson et al. 2001, 2011; Dearing 2008; Dearing et al. 2008; Ellis et al. 2013; Diaz et al. 2019). However, as human population growth and industrial technologies have accelerated in the past two centuries, anthropogenic impacts on the biosphere have led to unprecedented levels and rates of sustained change (Vitousek 1994). These anthropogenic stressors can interact synergistically with climate change to affect core ecological processes, including nutrient cycling, species phenology, population migration, and individual-level demography. For example, species or populations that have been reduced by habitat loss or overharvest might be pushed over demographic thresholds by climate shocks such as droughts or warming events (Pershing et al. 2015; Newbold 2018; Northrup et al. 2019).

A key challenge for ecosystem management is the continued expansion and layering of multiple anthropogenic stressors exacerbating ecological system change (Figure 1; Diaz et al. 2019). Collectively, these drivers can create novel ecosystems (Seastedt et al. 2008). For example, novel stream communities are increasingly common in the southwestern United States, where shifts to more drought-tolerant vegetation in riparian areas and introduced virile crayfish *Orconectes virilis*, which feed on organic matter and macroinvertebrates, are working together to reduce diversity of litter-dwelling communities in desert streams (Moody and Sabo 2013). Adaptation to ecosystem change is challenging, particularly given shifting baselines and increased unpredictability of system responses (Williams and Jackson 2007). As a result, future conditions will be much different than in the past, and as such, traditional management

Contributions to Ecosystem Change

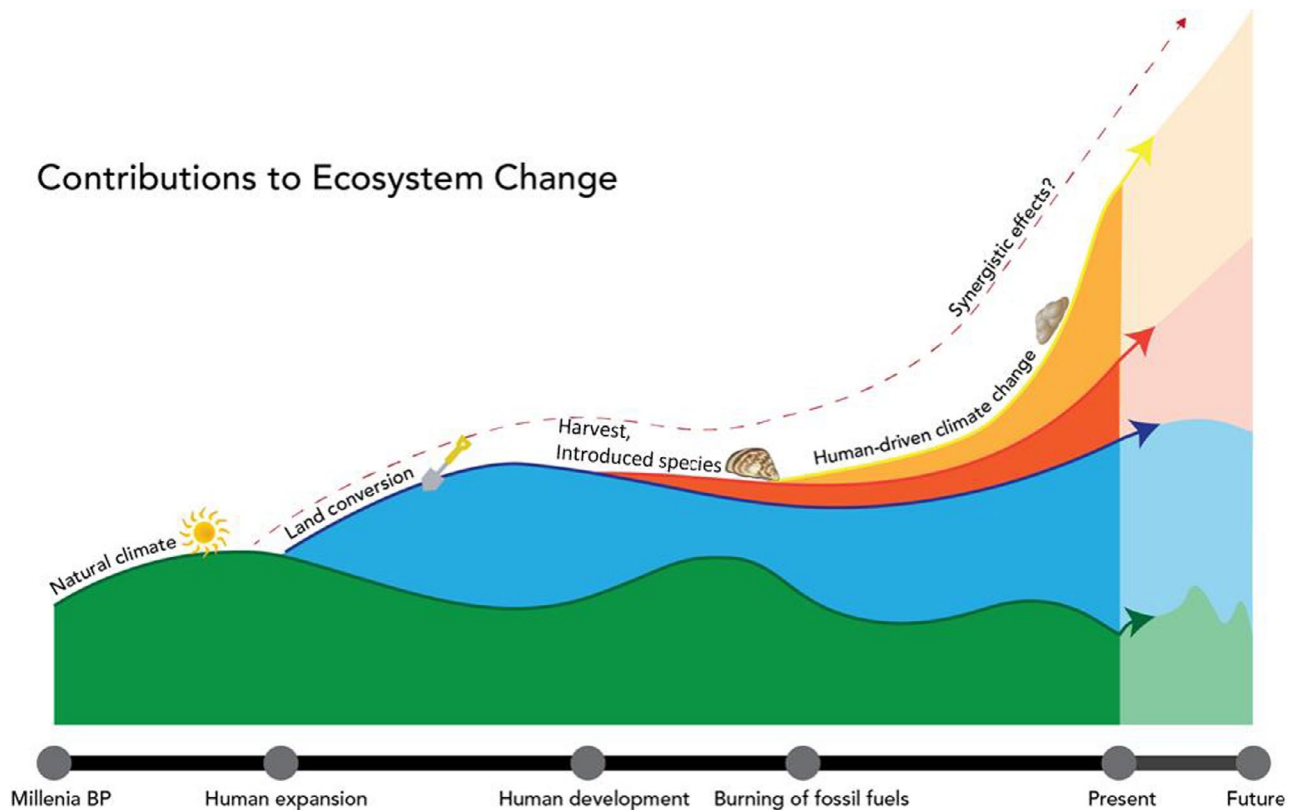


Figure 1. Conceptual illustration of combined effects of drivers of ecosystem state (and therefore factors that contribute to changing state) and how those have changed historically.

focused on the range of historical variability may have limited utility for conservation and management planning of future ecosystem states.

Climate change in the 21st century under even the most-aggressive greenhouse-gas reductions will drive widespread ecosystem change, and worst-case emissions scenarios may lead to ecosystem transformations of global extent (Nolan et al. 2018). New frameworks are needed for management in a world where transformations are more rapid, dynamic, and comprehensive than at any previous point in human history (Folke et al. 2002). We outline three alternative strategies for fish and wildlife managers to consider in addressing ecosystem transformation. We provide context for choosing among these strategies, including considerations of temporal and spatial scales, as well as magnitude of change. We also briefly describe sources of uncertainty associated with ecosystem transformation and provide guidance on how the three management strategies can be incorporated into a general planning process applicable to specific situations. Finally, we highlight key experience and knowledge gaps facing management for ecosystem transformation.

A MANAGEMENT FRAMEWORK FOR ECOSYSTEM TRANSFORMATION

A variety of management frameworks exist for responding to ecosystem change (e.g., Millar et al. 2007; Hobbs et al. 2009; Jackson and Hobbs 2009; Aplet and Cole 2010; Stephenson and Millar 2012; Stein et al. 2014; Truitt et al. 2015; Fisichelli et al. 2016a; Fortini and Schubert 2017). Some prior response frameworks, for example, have focused on managing states, characteristics, or attributes of a system, such as resilience

(e.g., National Fish Wildlife and Plants Climate Adaptation Partnership 2012). That term, however, has become increasingly ambiguous; it is interpreted differently among management sectors (Fisichelli et al. 2016a) and, in practice, may be confusing to managers attempting to select options to respond to change. We instead suggest a holistic, active framework that describes management responses appropriate under ecosystem transformation. Specifically, this active approach squarely assigns the adaptation response to a managerial decision: *resist*, *accept*, or *direct* the change (also see Aplet and Cole 2010; Stein and Shaw 2013; Fisichelli et al. 2016b; Aplet and McKinley 2017).

Depending on the rate and direction of change, we suggest that either:

- Ecosystem transformations can be **resisted**, because managers choose to promote the persistence of current or historical ecosystem composition, structure, and processes;
- Ecosystem transformations can be **accepted**, perhaps because they cannot feasibly be stopped, they are not sufficiently impactful to warrant a response, they are considered acceptable (perhaps even desirable) by stakeholders or society, or there is a lack of will or impetus to resist change despite sufficient knowledge and resources; or
- Ecosystem transformation can be **directed** towards a specific alternative ecosystem configuration, because resisting change appears to be impossible and feasible opportunities exist to steward change towards a more-desirable outcome than that anticipated from accepting the default trajectory of change.

These decisions (Figure 2) capture the range of responses by humans to address ecosystem change. Synonymous with

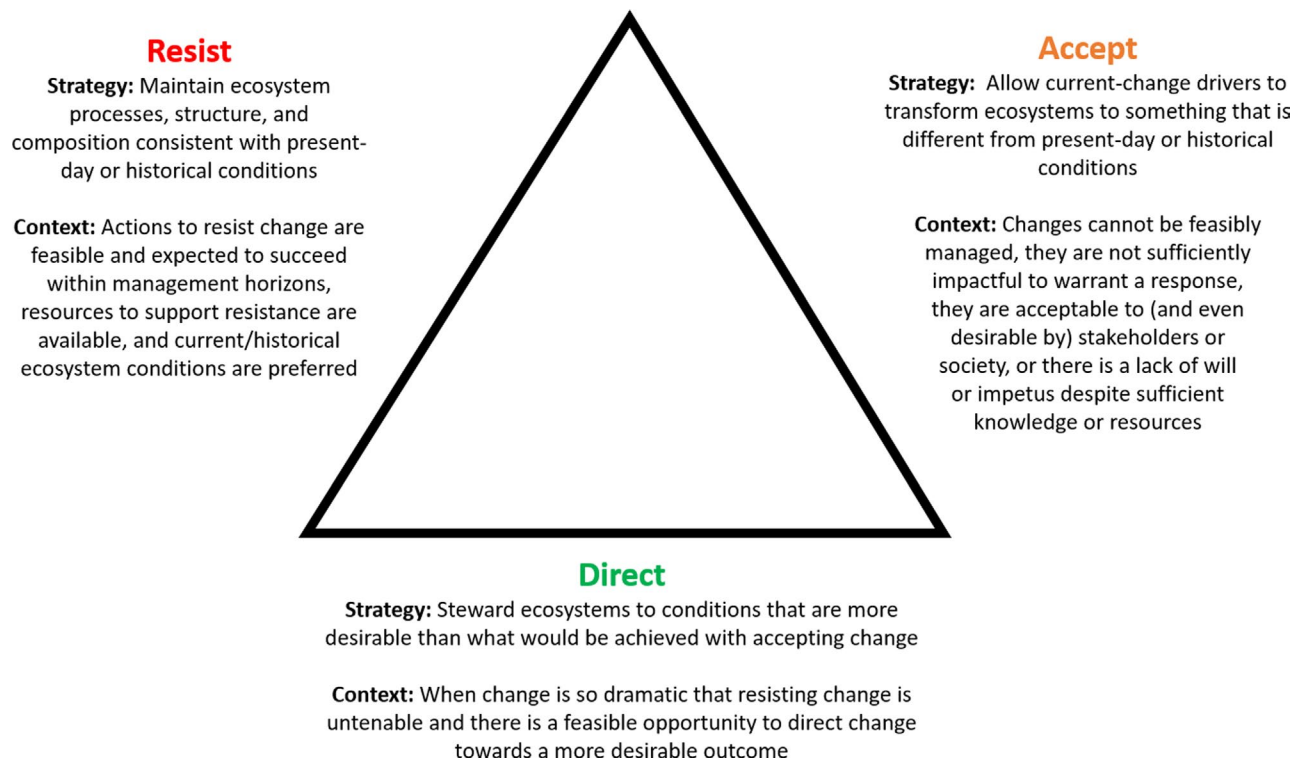


Figure 2. Management strategies and contexts for when one might *resist*, *accept*, or *direct* ecosystem transformation to promote a desirable outcome that is self-sustaining and self-organizing. These strategies are all-encompassing (i.e., nothing is left outside the decision space) and can be implemented simultaneously on different components of an ecosystem.

how Magness et al. (2011) defined retrospective and prospective adaptation, resisting works *against* climate change by attempting to maintain historical conditions, and directed change works *with* climate change trajectories by stewarding towards some altered future state. Accepting change should not be considered a passive choice. For example, a management decision to cease building an artificial dune system at Assateague Island National Seashore and allow for beach overwash is explicit acceptance of the ecological and economic impacts of rising seas and increasing storm frequency and intensity. Although the decision allows for barrier island migration, it does so with the added expense of rebuilding beachside visitor facilities further inland by the National Park Service and the loss of diked waterfowl impoundments that had been maintained for a half a century by the Chincoteague National Wildlife Refuge (USFWS 2015a).

Each of these three management options is meant to promote a desirable, or at least acceptable, outcome that is self-sustaining and self-organizing and does not require continuous intervention. Moreover, the three options are all-encompassing (i.e., nothing is left outside the decision space), and they can be applied either sequentially or concurrently for different components of the ecosystem. Having contrasting options allows for comparison among potential outcomes that may or may not correspond with a historical state. The three actions also collectively allow for management strategies to be diversified so that overall risk can be reduced (i.e., bet hedging). This framework can be applied by either focusing on outcomes (i.e., strategically) or on the means to achieve the outcome (i.e., tactically), and is easily incorporated into other planning processes, such as Climate-Smart Conservation (Stein et al. 2014).

Although resisting change is a common action used by natural resource managers, accepting and directing change are not considered traditional management strategies. Therefore, to demonstrate these options under ecosystem transformation, we provide case studies (Boxes 1–4) to show how natural resource managers are incorporating *resisting*, *accepting*, and *directing* complex ecological changes driven by warming climates in coral reefs of Florida, coldwater lakes in Minnesota, East Coast marshes, and ecosystems of southcentral Alaska.

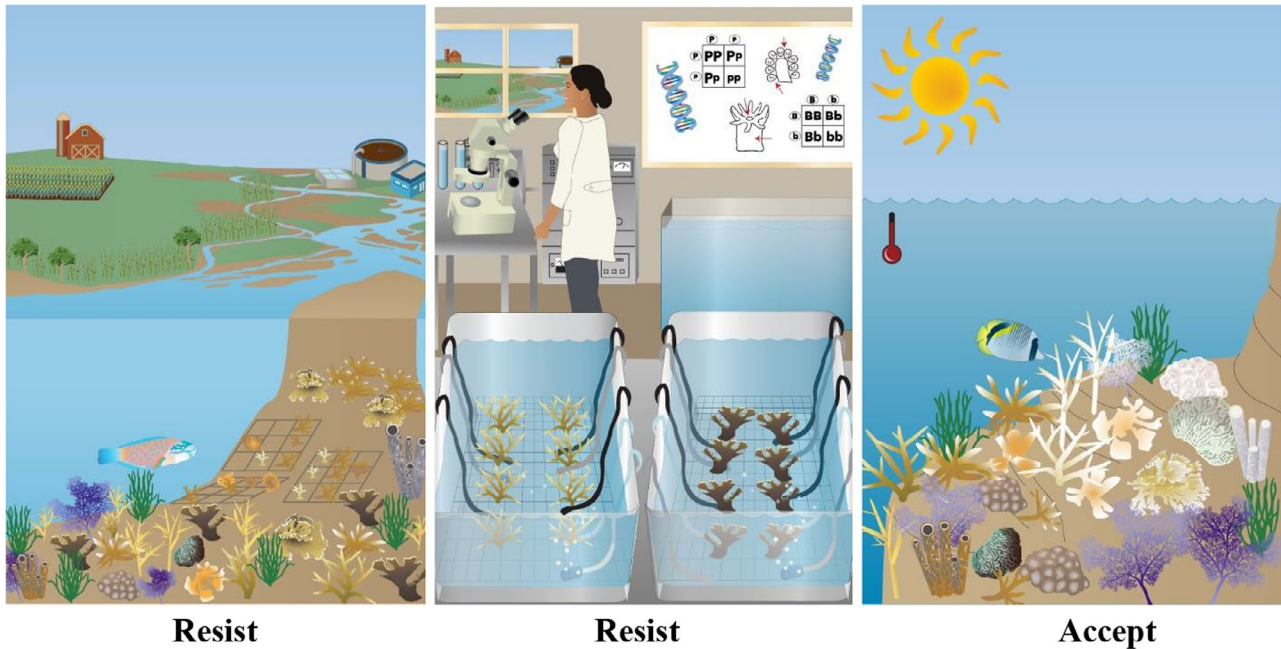
CHOOSING AMONG STRATEGIES

Choosing among *resist*, *accept*, or *direct* strategies to address ecosystem transformation relies on the ability to recognize that systems are changing, and to identify the key drivers of change. Decisions can be complicated because changes to species or functional groups may not occur in synchrony. Managers may have to implement multiple options concurrently to reach a desired outcome. Being explicit about a decision to *resist*, *accept*, or *direct* ecosystem change is an important first step in managing ecosystem transformation. Such deliberate choice can help prioritize research, monitoring, and action agendas tailored to implement a selected transformation strategy or prepare for future ability to switch strategies. Temporal and spatial scales, as well as magnitude of changes, are important considerations in deciding among the three strategies.

Time

Decision timelines and the speed of system change combine to influence the choice to *resist*, *accept*, or *direct* trajectories of change. Resisting ecosystem transformation may be only a temporary, short-term solution, unless the drivers of

Box 1. A multipronged approach to coral restoration in the Florida Reef Tract.



The Florida Reef Tract (FRT), the only tropical coral reef system in the continental USA, is undergoing transformation. The FRT is inhabited by over 500 fish and thousands of invertebrate species (Shinn et al. 1989; Lirman et al. 2019) and FRT ecosystem services (e.g., coastal protection, sand supply for beaches and fisheries) are crucial to the economy of south Florida, where coastal tourism and fishing generate US\$6 billion per year (Ault et al. 2014). Two species of branching corals, *Acropora palmata* and *A. cervicornis*, and a massive genus, *Orbicella* (formally known as *Montastrea*) have historically been the predominant reef-building corals of the FRT (Precht and Miller 2007). Sufficient coverage of reef-building corals is essential for reef biodiversity and ecosystem services (Moberg and Folke 1999), but their coverage has decreased dramatically over the last 30–40 years in the FRT (Alevizon and Porter 2015). *Acropora* and *Orbicella* taxa mortality has largely driven coral cover losses, but overall coral richness has also decreased (Porter et al. 2002; Lirman et al. 2019). Coral losses are attributed to increasing ocean temperatures (Kuffner et al. 2015), nutrient pollution (Vega Thurber et al. 2014), sedimentation (Miller et al. 2016) and overfishing, but the synergistic effects of extreme temperature-induced coral bleaching and diseases may be the major cause of coral declines, globally (Aronson and Precht 2006). As scleractinian corals decline, FRT reefs have shifted to an octocoral (i.e., soft corals, sea fans), and sponge-dominated community structure (Ruzicka et al. 2013; Alevizon and Porter 2015). Some site-specific increases of algal cover have occurred but algal phase shifts are less prevalent in the Florida Keys than many Caribbean locations (Bruno et al. 2009).

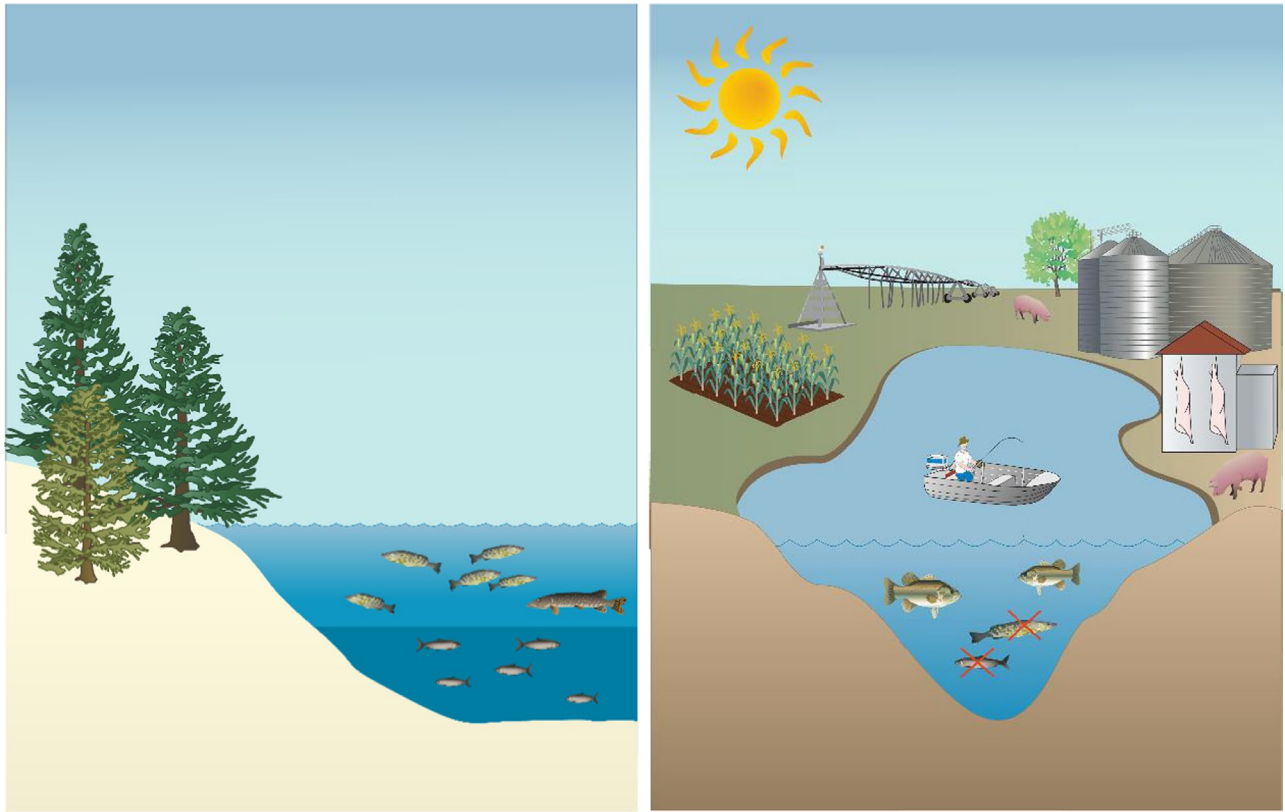
Resisting transformation is the central management response to the loss of reef-building corals within this ecosystem, and a wide variety of efforts with this aim have been pursued in the FRT. These include nutrient pollution and fisheries regulations, and restoration via coral propagation and outplanting. The Comprehensive Everglades Restoration Plan and U.S. EPA's collaborative efforts with the Florida Keys National Marine Sanctuary are attempts to decrease sewage and agricultural nutrient inputs that favor algal growth (Causey 2002; Precht and Miller 2007). Fishing regulations and preferences have maintained high herbivorous fish biomass in the Florida Keys, relative to the rest of the Caribbean, and grazing control is hypothesized to partially explain the relatively low macroalgal cover in the Florida Keys (Aronson and Precht 2006; Bruno et al. 2009). The collaborative coral propagation and restoration programs at Mote Marine Laboratory, the Coral Restoration Foundation, NOVA Southeastern University, the University of Miami, the Florida Fish and Wildlife Conservation Commission, and The Nature Conservancy all aim to restore previously dominant reef-building corals and resist ongoing coral cover loss (Lirman et al. 2019). Initial work focused on asexual propagation of clonal fragments of fast growing *A. cervicornis*, but new techniques have been developed to asexually propagate slower-growing massive stony corals (Page et al. 2018). Outplanting corals with known ecological resilience to anticipated conditions such as heat-stress, acidification, and disease is the “next frontier” for resistance via coral propagation. In the future, assays and habitat indicators may be used to select resilient wild stock for nurseries (Morikawa and Palumbi 2019). A collaboration between researchers in Australia and Hawaii is exploring selective breeding, trans-generational and intergenerational acclimatization, symbiont modification, and interspecific hybridization to initiate “human assisted evolution” in corals (coralassistedevolution.com; van Oppen et al. 2015). Additionally, there is recognition that coral restoration programs that previously focused on a few genera of fast growing coral species that cover large areas quickly, but also had high susceptibility to thermal stress, should utilize corals that will be robust to future anticipated conditions (Rinkevich 2015).

While resistance is the focus of efforts to reduce change in the FRT, some climate-related mass mortality events and associated shifts in community composition may have to be *accepted* if global sea surface temperatures are allowed to fluctuate outside of historical ranges. Two back-to-back mass bleaching events during summertime warm temperature anomalies in 1997–1998, and 2014–2015, and a cold-water event in 2010 have caused recent mass mortality (Ruzicka et al. 2013; Kuffner et al. 2015). Octocorals, while susceptible to many of the same stressors as the historically abundant hard coral species, are less prone to bleaching in warm temperatures and appear to recover more quickly so their relative abundance may increase following major bleaching events (Ruzicka et al. 2013). Directed transformation to an alternate benthic community is not a current management strategy or goal in the FRT and, to our knowledge, has rarely been considered as a management option for coral reef ecosystems. However, directed transformation of an adjacent temperate community that is warming to facilitate coral establishment is a theoretical option. Given the “tropicalization” of marine coastlines and the widespread decline of corals in many parts of their current distribution, choices will likely be made about whether to facilitate the poleward spread of corals into temperate systems (Vergés et al. 2019).

change are addressed. For example, attempts to eradicate invasive species may only delay their eventual establishment, unless propagule pressure is halted (Mack and Lonsdale 2002).

Conversely, we may need to reconsider conventional invasive species management in a “post-native” world (Hill and Hadly 2018). Directed ecosystem change requires managers to

Box 2. Changing fish communities in the Great Lakes basin.



Resist

Accept

Environmental conditions in the Laurentian Great Lakes and associated Great Lakes basin are likely to shift considerably because of warming temperatures, introduced species, and changes in nutrient runoff (Rahel and Olden 2008; Michalak et al. 2013). These changes can negatively affect forage fish communities that support top lake predators, including Walleye *Sander vitreus*, Northern Pike *Esox lucius*, Muskellunge *E. masquinongy*, and Lake Trout *Salvelinus namaycush*, as well as having implications for a popular sportfishing industry. Cisco *Coregonus artedii*, for example, is a stenothermic salmonid distributed in Canada and the northern United States and is important prey for many top predators, including Walleye, a popular game fish in the region. Cisco rely on the cold, oxygenated hypolimnetic water of lakes, particularly during summer periods when surface waters warm and stratify. Cisco populations in Minnesota, at the southern region of its geographic range, are declining, most likely as a result of warming water temperatures (Jacobson et al. 2012). Further Cisco population losses are imminent as warming continues (Fang et al. 2012).

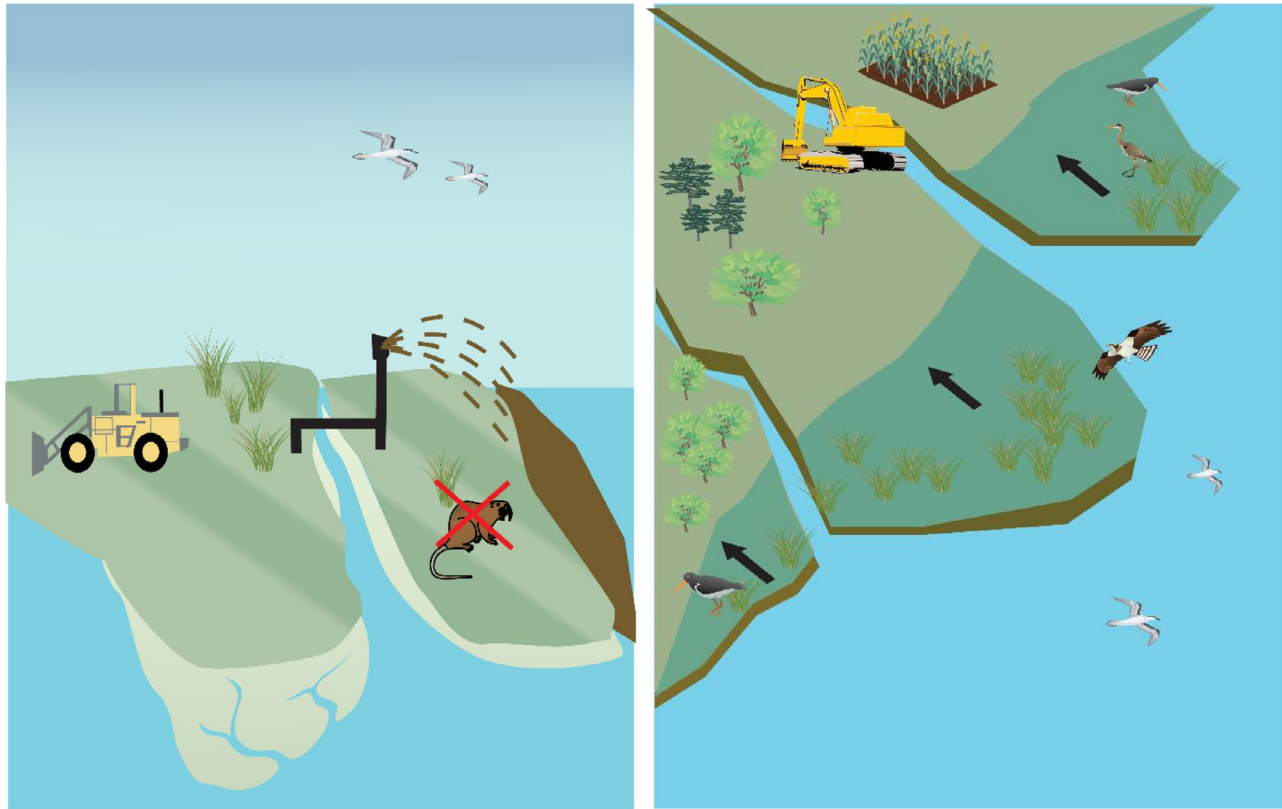
In recent years, Minnesota Department of Natural Resources (MN DNR) developed a habitat model to identify 171 refuge lakes where the deep-water layer is projected to remain sufficiently cold and oxygenated in late-summer, even during the longer duration of stratification projected with climate change (Jacobson et al. 2013). Managers can *resist* climate-induced loss of Cisco in these deep, clear refugium lakes as long as their water quality remains high. To this end, managers are actively pursuing conservation easements and other land protection mechanisms to protect the watersheds of these lakes from development. Land conversion of these contributing watersheds would likely increase their nutrient and sediment loads, jeopardizing the deep oxygenated hypolimnetic layer that cisco depend on. It is MN DNR's goal to maintain >75% of the watershed of these refugium lakes in a forested state.

To prioritize protection efforts and engage in strategic *resistance*, Jacobson et al. (2013) sorted refugium lakes supporting healthy Cisco populations based on threat (i.e., likelihood of land use change, existing levels of protection) and investment efficiency (i.e., total surface area of lake per dollar invested). Based on their analysis the forested ecoregion of northcentral Minnesota was identified to contain high return-on-investment cisco lakes. An overall estimated US\$156 million would be needed to achieve watershed protection goals for all MN DNR's refugium lakes that are not yet protected (Jacobson et al. 2013). Although securing adequate funding to achieve these protections initially seemed unlikely, Minnesota passed a law in 2008 to allocate one-eighth of 1% of sales tax revenue to conservation efforts, representing \$190 million per year, greatly enhancing the prospect of achieving success in this work (Jacobson et al. 2013). As of 2018, \$11.7 million has been allocated to conservation easements to protect priority lakes from change. In Minnesota's southernmost lakes, agricultural land use likely exacerbates climate warming, while also introducing significant nutrient loads into those systems (Jacobson et al. 2013). Managers acknowledge the decline of Cisco (and associated consequences to the food web and sportfishing) in many of these lakes and may choose to *accept* changes, given the higher cost of conservation efforts in these areas. In turn, this acceptance acknowledges that warmwater species, such as Largemouth Bass *Micropterus salmoides* and Smallmouth Bass *M. dolomieu*, are increasing. Bass can better compete for existing food resources in warmer waters and have the potential to support a popular sportfishing industry that has historically been focused on other species (<https://bit.ly/2CH5ywy>).

consider an ecosystem's position on its trajectory of change, what preferred state to aim for, how long it will take to achieve, and by what means it could be accomplished. The latter may include identification of key points for intervention to alter or maintain the trajectory.

An "active" strategy will be required that guides the course of transformation by establishing core ecosystem functions so that ecosystem dynamics stabilize in a desirable configuration. Directing change may be deemed unfeasible if the ecosystem has already changed enough that diversion to another path

Box 3. Facilitating upslope marsh migration on Blackwater NWR.



Resist

Direct

The 11,300-ha Blackwater National Wildlife Refuge in rural southern Dorchester County, Maryland, is part of the Chesapeake Bay National Wildlife Refuge Complex. The refuge is connected to saltwater by the tidal Blackwater and Transquaking rivers that flow into Fishing Bay on the eastern shore of Chesapeake Bay. Colonists drained much of the surrounding lands in the 17th and 18th century for agriculture and forestry, both of which are still mainstays in this area. Blackwater Refuge was established in 1933 under the Migratory Bird Conservation Act “for use as an inviolate sanctuary, or for any other management purpose, for migratory birds.” Because adjacent lands have since been added to the refuge, the legislative mandates have also expanded to include broader threatened and endangered species conservation, as well as other wildlife conservation.

Blackwater Refuge has very low and flat topography, with elevations ranging from below mean sea level to 2.5 m above mean sea level. Consequently, sea-level rise (3.44 mm/year) is almost twice the global average (1.8 mm/year) and has had catastrophic effects on tidal saltmarsh. Between 1938 and 2006, Blackwater Refuge lost 2,030 ha of wetlands to open water at a rate of 30 ha/year (Scott et al. 2009). That loss occurred initially in three-square bulrush *Schoenoplectus americanus* tidal marsh at the confluence of Little Blackwater and Blackwater rivers, and subsequently progressed both upstream and downstream. Land subsidence, post-glacial rebound, saltwater intrusion, and severely modified hydrology played a role in wetland losses, which were exacerbated by excessive herbivory from introduced nutria *Myocastor coypus* and mute swans *Cygnus olor*, and resident Canada geese *Branta canadensis* (USFWS 2006). During the same period, Blackwater Refuge gained 1,090 ha of new marsh along the upland edge, presumably through upslope migration of tidal marsh as seas rose (Scott et al. 2009; Lerner et al. 2013).

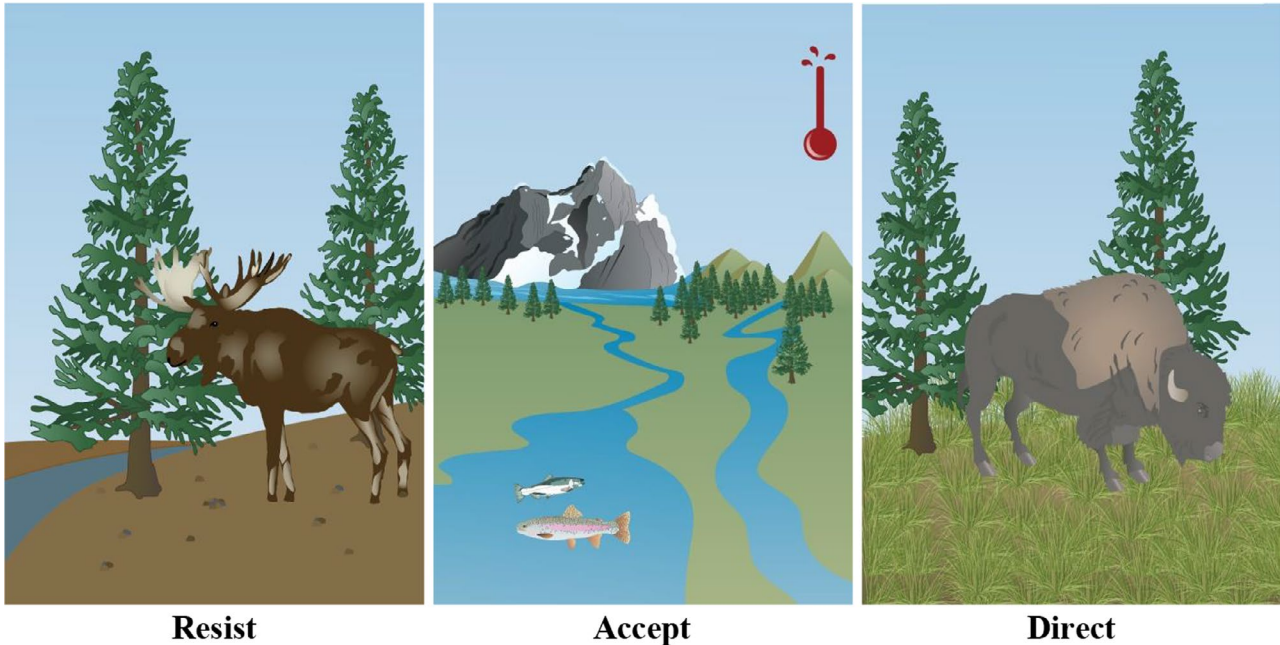
Working closely with partners, including The Conservation Fund and Audubon Maryland-DC, Blackwater Refuge staff responded with different approaches based on recent sea-level rise modeling. In *Blackwater 2100: A Strategy for Salt Marsh Persistence in an Era of Climate Change* (Lerner et al. 2013), a portfolio of *resisting* and *directing* change options were recommended including sediment enhancement, shallow drainage of waterlogged areas, invasive species control, and promoting marsh creation through upland slope migration (Lerner et al. 2013). As a *resistance* response to actual and modeled future loss of brackish marsh near Shorter’s Wharf, the partnership recently completed a 16-ha project where dredged material was sprayed in a thin-layer over the surface of the marsh, building elevation and enhancing plant vigor and productivity (USFWS 2015b). Also, through an intensive trapping program by USDA Wildlife Services, nutria have nearly been eradicated from the Delmarva Peninsula (<https://bit.ly/3eBo1HX>). Eliminating this additional stressor has allowed for increases in native vegetation, including three-square bulrush, and thus assisted with marsh recovery and expansion.

The refuge has acquired almost 300 ha of adjacent private lands to allow for marsh migration. Outside the refuge, on Farm Creek Marsh, which is owned and managed by the Chesapeake Audubon Society, a US\$475,000 demonstration project *directs* change, accelerating tidal marsh migration into low-lying farm lands using a low ground-pressure excavator to extend the head of a nearby tidal creek 400 m, which will reduce inundation, introduce tidal exchange and reinvigorate marsh vegetation (<https://bit.ly/2ZEafAf>).

would be difficult, the timeframe for reaching the desired state is very long, or the time goal is unrealistically short. Being explicit about the temporal trajectory will promote creativity (e.g., consideration of a range of options and potential controls) and bet hedging when managers recognize competing options for management responses with varying uncertainty. Finally, the choice to accept change applies across all time

scales and is, in fact, the default strategy in the absence of either deliberate management for ecosystem transformation or active resistance to change. Ecosystem management timelines can also combine approaches. For example, resisting change can be used to buy time for planning subsequent directed change, preparing for inevitable ecosystem transformation, or gathering more information to guide decisions.

Box 4. A land management portfolio in response to multiple climate stressors on the Kenai Peninsula, Alaska.



Encompassing both boreal and coastal rainforest biomes, three icefields, and an elevational range from sea level to > 1,600 m, the 24,300-km² Kenai Peninsula juts into the Gulf of Alaska, connected to mainland Alaska by a 16-km wide mountainous isthmus. The peninsula is home to the celebrated Kenai River, the Kenai National Wildlife Refuge, Kenai Fjords National Park, and Chugach National Forest. As climate warming has accelerated over the past half century, available water has declined 55% (Berg et al. 2009), trees and shrubs have encroached into alpine tundra 1.0–2.8 m per year (Dial et al. 2007, 2016), wetlands have decreased 6 – 11% per decade in surface area (Klein et al. 2005; Berg et al. 2009), and the Harding Icefield has lost 5% in surface area and 21 m in average elevation (Adalgeirsdóttir et al. 1998). The historical regime of forest fires in summer now includes grassland fires in spring, prompting Alaska’s official fire season to be declared a month earlier (Morton et al. 2006). Water temperatures in some nonglacial streams already exceed physiological thresholds for salmonids during July (Mauger et al. 2017) and fry abundance, size, and overwinter survival in glacial lakes declined as a result of increasing glacial silt, decreasing euphotic zone, and decreasing copepod biomass (Edmundson et al. 2003). American marten *Martes americana* recently colonized the Kenai Lowlands, responding to warmer winter nights, despite poor subnivean conditions (Baltensperger et al. 2017), and at least 27 new bird species have been detected since 2012 (ebird.org/home).

Climate envelope modeling portrays a future landscape by 2100 that is very different from what now occurs on the peninsula. Alpine tundra may be replaced by encroaching forests, with forecasts for lower elevations ranging from more hardwood species to catastrophic deforestation (Magness and Morton 2018), exacerbated by a spruce bark beetle *Dendroctonus rufipennis* epidemic and sustained by consecutive summers of above-average temperatures (Berg et al. 2009). Natural resource agencies and organizations on the Kenai Peninsula have responded inconsistently to climate change (Hansen 2014; Magness and Morton 2017). Most of the aforementioned changes have been *accepted* by natural resource managers (albeit implicitly), either because they are infeasible to manage (e.g., changes in bird migration, glacial ablation) or they are not impactful enough to warrant a management response (e.g., afforestation, American marten establishment).

Some changes have been *resisted*. In the aftermath of beetle-induced tree mortality, the Kenai Peninsula Borough and Ninilchik Native Association reforested > 1,000 ha in plantations with both native (e.g., white spruce *Picea glauca*) and nonnative species (e.g., *Pinus contorta*); *P. contorta* was introduced after the Swanson River fire approximately 50 years ago (Morton 2017). In response to the fuel created by grass replacing beetle-killed spruce along the wildland-urban interface, an interagency fire management working group is developing control treatments for *Calamagrostis canadensis* (Wahrenbrock 2009). Warming waters in the Anchor River have triggered the Kachemak Heritage Land Trust, partnered with Cook Inletkeeper, to acquire riparian parcels that harbor cold-water refugia for salmon, which were detected from aerial thermal-infrared imagery (<https://bit.ly/32wzF10>). Finally, four species of invasive plants are targeted for eradication (*Elodea* spp., *Melilotus alba*, *Viccia cracca*) or containment (*Phalaris arundinacea*) after rapid introduction onto this Alaskan landscape, even as more than 100 species are already accepted as too widely distributed for peninsula-wide management goals (e.g., *Taraxacum officinale*; Slemmons 2007).

Elsewhere on the Kenai Peninsula, others, including the lay public, are *directing* change. Sitka black-tailed deer *Odocoileus hemionus sitkensis* are likely to colonize the peninsula in the near future as snow cover decreases at low elevations (Morton and Huettmann 2017). In response to rapidly increasing growing days, local communities, rural landowners, and farmers have planted more than 61 exotic tree species for landscaping (e.g., *Quercus* spp., *Fraxinus* spp., *Acer* spp., *Pinus* spp., *Larix* spp., *Metasequoia glyptostroboides*, *Thuja* spp.) and fruit production (e.g., *Pyearus ussuriensis*, *Prunus* spp., *Malus* spp.) in an Alaskan ecosystem that supports 14 native tree species (Morton 2017). Extensive deforestation on the southern peninsula caused by spruce bark beetles, coupled with wildfire, has prompted the Kenai National Wildlife Refuge to consider introducing foundation species (Record et al. 2018) to promote higher biodiversity via niche, structural, and compositional diversification in this developing novel (albeit depauperate) grassland ecosystem (Bowser et al. 2017). This approach could be manifested as the use of prescribed fire and the introduction of a nonnative grazer such as wood bison *Bison bison athabasca* to steward the system towards a richer grassland, or the planting of nonnative trees that are resistant to spruce bark beetle (e.g., *P. contorta*) to promote a more resilient forest ecosystem.

Although ecosystems encompass social and ecological dynamics, these processes often occur at different time scales (Cumming et al. 2006; Beever et al. 2019). Rapidly changing social dynamics often force longer-term ecological transformation. For example, by the 1980s, fisheries managers had

established nonnative Pacific salmon *Oncorhynchus* spp. in the Great Lakes to control Alewife *Alosa pseudoharengus*, an invasive forage fish. This led to rapid development of a Pacific salmon sportfish economy, entrenching social values for nonnative fish and transforming the socioecological system (Tanner and

Lynch 2014). Presently, managers are pressured to maintain this precarious balance between Alewife and Pacific salmon, hampering options to restore suppressed native fish communities that may be more ecologically resilient to ongoing ecosystem changes in the Great Lakes (e.g., changing climate; Dettmers et al. 2012). Consequently, the fastest-occurring changes may most strongly impact management under ecosystem transformation, because it is difficult to implement actions in a short time period.

Space

The tractability of the management objective (e.g., resources needed to assess, design, implement, and monitor management actions) is driven by the spatial scale and complexity of ecosystems under management. Small spatial extents are conducive to single, intensive efforts with limited budgets, staff time, or equipment, but can be impacted by spillover from neighboring regions that may be managed differently (i.e., edge effects; Liu et al. 2018).

Operating at large spatial extents can be daunting when considering the costs and logistics of management. An often-greater diversity of physical, chemical, and biological attributes within a large region can mean that small-scale pilot projects used to test responses to management actions may not adequately represent the variety of conditions and broader-scale suite of responses when scaled up. Managing ecosystem transformation at larger spatial scales may also be more prone to constraints imposed by laws or jurisdictional boundaries and require governance changes to accommodate management interventions (Beever et al. 2014; Pinsky et al. 2018). This may also require engaging a greater number of stakeholders with potentially disparate ecological and socio-cultural priorities (Allen and Gunderson 2011).

Management at spatially extensive scales may also have benefits for responding to ecosystem transformation. Control over a larger area can align the spatial scale of management interventions with the scale of ecosystem transformation, reducing the challenges of disparate management regimes within the same transforming system. Large spatial extents may also allow for combining approaches through time, such as using resistive actions to maintain species refugia and ecosystem-services reserves, while planning for future transformative change. Further, although leading- and trailing-edge populations are both important for species persistence under climate change (Rehm et al. 2015), managers often have to prioritize one edge population over the other or over the center of the distribution. Working at greater spatial extents can reduce the probability of only working with a limited portion of the geographical distribution (Beever et al. 2014).

Magnitude

In addition to the variability in spatio-temporal scales, there are varying degrees of magnitude of ecological transformations. Ecosystems can be conceptualized in terms of nested levels of biological organization along three axes: ecological structure, composition, and function (Noss 1990). Along each axis, the levels of ecosystem actors include genes, populations and species, communities and ecosystems, and sea-, river-, or landscapes. Some ecosystem transformations may involve changes in only a single keystone or foundational species, cascading to broader changes in ecological function and structure (Pureswaran et al. 2015; Colloff et al. 2016).

When multiple species within a guild or numerous functional groups in a community are involved, ecosystem transformation is greater in magnitude. As with single-species transitions, changes to guilds or functional groups that include dominant plant species or form the base of the food web (e.g., copepods; Friedland et al. 2013) can initiate cascades that affect other ecological functions and species (e.g., Martínez-Vilalta and Lloret 2016). In the most comprehensive transitions (e.g., from forest to savanna; Silva 2014), many of the species typical of the former community or ecosystem are no longer present in the new system. Such whole-community transformations can be rapid, occurring when: (a) contemporary climate change shifts a landscape into a new biome (Lugo et al. 1999; Williams and Jackson 2007; Nolan et al. 2018), (b) invasive species, biogeochemical alterations, or severe disturbances (natural or anthropogenic) transform the ecosystem to a novel state (Scheffer et al. 1993; Hobbs et al. 2009, 2014), or (c) when successional trajectories following disturbances are redirected by environmental changes to new, self-sustaining states (Johnstone et al. 2016; Guiterman et al. 2018; Davis et al. 2019).

UNCERTAINTY ASSOCIATED WITH ECOSYSTEM TRANSFORMATION

Management amidst ecosystem transformation occurs within a matrix of high uncertainty, encompassing gaps in fundamental understanding of ecosystems and uncertain outcomes of alternative management actions. System uncertainty derives in part from the high variability and complex dynamics typically found in ecosystems, particularly when driven by multiple and probably interacting anthropogenic or climatic stressors that vary spatially and temporally (e.g., Anderson et al. 2008; Jackson et al. 2009; Dobrowski et al. 2013). Ecosystems are complex, and they often have multiple possible trajectories and endpoints (Chapin et al. 2010). Coupled with the difficulty and expense in observing these complex systems, our collective ability to characterize and predict ecosystem dynamics is often poor, leading to considerable model uncertainty and statistical imprecision (e.g., Hilborn 1987). For example, validating models of future ecosystem dynamics with empirical data is complicated by the lack of locally current analogs (Williams et al. 2007). However, others have used heuristic approaches to address uncertainty (e.g., Magness and Morton 2018). Given available knowledge, outcomes of management actions are also often uncertain, such that they may be difficult to observe or can play out in unexpected ways (Hiers et al. 2016). Finally, unexpected and sudden system transformations can and do occur, potentially rendering existing system knowledge and management experience insufficient under novel system structure and function (Beever et al. 2013; Fernández-Llamazares et al. 2015).

GUIDANCE FOR IMPLEMENTING *RESIST, ACCEPT,* AND *DIRECT* STRATEGIES

Natural resource management typically focuses on achieving a “fixed” goal and an associated set of objectives, implicitly assuming stationary variation around a mean ecosystem state (Jackson 2012). Effective management will need to amalgamate processes for structured, objective decision making with processes for adaptive learning as ecosystems change and knowledge improves (Holling 1978; Walters 1986; Nichols et al. 2011). This will require engagement of key stakeholders who strive to reach agreement on measurable and achievable

objectives and relevant management actions across jurisdictional boundaries and through time. The use of support tools (e.g., scenario planning; Runyon et al. 2020) will be useful for promoting stakeholder dialog and clarifying management priorities. Because management resources are always limited, long-term datasets designed to detect system shifts and increases in variability, as well as data flows supporting mechanistic understanding of system dynamics (i.e., how and why systems are changing), may be high priority for provisioning managers with the information they need to both address transformations and select adaptation actions. However, information may perpetually lag changes in the system under ecosystem transformation. Consequently, course corrections or experimental approaches in management may be needed, particularly in light of rapid environmental or system changes already underway. Finally, responses to ecosystem transformation may differ greatly in their feasibility. Potential decision pathways related to implementation are explored by Lynch et al. (*submitted*).

A PATH FORWARD

Key knowledge needs to support effective management of ecosystem transformation include:

- *Stakeholder engagement.* Ecosystem transformation increases the difficulty of defining and updating management goals. Improved techniques to coordinate among stakeholders and structure efficient decision making will be critical for both enabling deliberate management under ecosystem transformation and avoiding paralysis.
- *Assessing the ecosystem.* Identifying indicators and setting management targets and thresholds will be important for assessment of ecosystem changes (Beever 2006; Levin et al. 2009; Samhuri et al. 2010).
- *Monitoring.* Monitoring will continue to be essential for tracking ecosystem trajectories and detecting when systems reach a new state, pass a known social or ecological threshold, or otherwise require a management course correction. However, monitoring is costly and resources may be stretched thin. Development of cost- and time-efficient monitoring technologies is urgently needed. For example, next-generation sequencing allows rapid and inexpensive assessment of changes in species assemblages (Bowser et al. 2017; Sikes et al. 2017). Though there are no “silver bullet” indicators that provide information on all the complexity of ecological systems (Landres 1992), monitoring of multiple keystone, umbrella, and foundation species can collectively indicate important changes in ecosystem function. Additionally, the timely collection of high-resolution and multispectral remote-sensing data may be necessary for monitoring large-scale changes (e.g., Elmendorf et al. 2012; Pettorelli et al. 2016).
- *Mechanistic understanding of system drivers.* Although empirical data can be used in many cases for making management decisions, increasing mechanistic understanding of system drivers (e.g., through experimentation) can be useful to project change and to design management (e.g., climate-adaptation) actions to resist or direct transformation, or to inform the implications of accepting it.
- *Flexibility or responsive management.* In many ecosystems, poor forecasting performance, increasing system uncertainty, and lack of options to control change over the near- or mid-term will prevail. Thus, development of flexible and responsive management strategies to cope with high uncer-


tainty will be important for buffering against inevitable or unexpected ecosystem transformation.

- *Directing change.* Resisting change is likely not a long-term solution in many ecosystems and accepting eventual transformation may not always be desirable. Continued experience with directed change will be critical for enabling this “active” management approach and may require the courage to implement management experiments, potentially at stepped levels to allow for course corrections.

ACKNOWLEDGMENTS

We thank Bill Dennison and Yesenia Valverde of the University of Maryland’s Integrated Application Network for facilitating our group workshop and assisting with figure development. Erinn Muller of the Mote Marine Laboratory and Aquarium provided valuable information for our case study on coral reefs. The Navigating Ecosystem Transformation on Federal Lands (FedNET) working group built a valuable intellectual foundation for this work. We also thank Wendy Morrison of the National Oceanic and Atmospheric Administration and two anonymous reviewers for critical comments that markedly improved the manuscript. All icons were obtained from the University of Maryland Center for Environmental Science (www.ian.umces.edu/imagelibrary/). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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