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Movers and stayers: novel assemblages in changing environments

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Increased attention to species movement in response to environmental change highlights the need to consider changes in species distributions and altered biological assemblages. Such changes are well known from paleoecological studies, but have accelerated with ongoing pervasive human influence. In addition to species that move, some species will stay put, leading to an array of novel interactions. Species show a variety of responses that can allow movement or persistence. Conservation and restoration actions have traditionally focused on maintaining or returning species in particular places, but increasingly also include interventions that facilitate movement. Approaches are required that incorporate the fluidity of biotic assemblages into the goals set and interventions deployed.

Occupy, vacate, or persist?

Conservation has a dual focus on places and species. Places include nature reserves, national parks and other open spaces that people manage for conservation outcomes. Individual species, and increasingly ecological communities, are the focus of legislation in many jurisdictions, via endangered species, biodiversity and wildlife conservation acts. Much attention and funding for conservation is directed at charismatic species, which often define the places (e.g., Serengeti, Sequoia National Park), and at biodiverse places (e.g., Cuatrociénegas, Kogelberg). This dual focus works well in a static world where species are found in particular places, but breaks down when places change and species move. With global change, particularly climate change, any particular place at any given time will have species that are staying put for the time being, and other species that are either invading or vacating. These phenomena are not new [1-3] (Box 1), but current and future environmental changes may be unprecedented in rate, magnitude and comprehensiveness [4-6] and in the levels and variety of human interventions. Much has been written about changes in species distributions in response to current and future climate change and other environmental changes [7-9] and the human role in engineering change through transport of species outside their normal ranges. This deliberate transport includes transport of potentially invasive species [10, 11] and assisted migration of species at risk [12-14].

In discussions of species responses to environmental change, particularly climate change, considerably less attention has been paid to the inverse situation, namely species populations that persist *in situ* in the face of environmental change. In the same way that some species move on their own and some are moved by humans, the stayers include species that persist on their own and others that stay owing to human actions or interventions. Some stayers may, in the absence of intervention, ultimately undergo extinction [15].

Species assemblages under environmental change thus comprise mixes of stayers (some of which are doomed to eventual extinction and some which will persist), and movers, which invade and expand at different rates. The transient dynamics of current-day ecosystems and assemblages that result from these species mixes have received relatively little attention [7]. Species distribution modelling has focused almost exclusively on single species, and inclusion of mechanistic consideration of how species interactions will affect outcomes remains challenging [16-18]. Where species assemblages are considered, indications are that individualistic species responses to climate and other changes will result in assemblages of varying degrees of novelty, ranging from not novel (e.g., similar communities already occur elsewhere) to completely novel species combinations (e.g. [19]).

In this paper we provide an overview of the various categories of species from the perspective of whether they are movers or stayers in a changing world, and we consider what this means for management and conservation. Although species and community dynamism are implicit in many aspects of ecology, including metapopulation biology, island biogeography and the like, current work on dynamics in the face of global change tends to focus on particular aspects of this dynamism. Different modes of movement (or lack thereof) are seldom considered together as a portfolio of possible responses. And by extension, there is relatively little attention to comprehensive consideration of the suite of possible management options in conservation and restoration arising from consideration of the array of species responses.

Moving and staying: responses to environmental change

Species ranges can stay the same, expand or contract over time (Figure 1a). Range contractions result from loss of local populations and may foreshadow species extinction [20]. Geographic extent of ranges may also stay the same overall while infilling or fragmenting within the broader boundary. In directional change, the range contracts at one end and expands elsewhere [21]. Range contraction may leave relict populations in persistent or transient refugia, [22-24], and fragmentation can reduce distributions to scattered, isolated patches. Range retreat may arise simply by the death of individuals *in situ*, or through emigration, whereas range advance generally necessitates immigration and colonisation, as well as subsequent population growth and infilling.

Particular species may contract and expand simultaneously in different regions. Every emigrant becomes an immigrant if it makes it somewhere else. Similarly, in any particular place, there may be a variety of dynamics occurring at any given time, with some species coming in on their own or by human translocation, some species remaining, and some species disappearing or moving elsewhere. Here, we examine the range of situations in which species can be either movers or stayers, recognising that these categories are not necessarily mutually exclusive.

Movers

Species can either move by themselves in response to environmental change or be moved by humans (Figure 2).

1. Species that move by themselves

Species move all the time: they often move extensively within home ranges, disperse over short and long distances. Many migrate seasonally, often over great distances, and at sufficiently long timescales, most shift their ranges in response to climate change. Species dispersal can occur in a number of different ways using an array of pathways and at a range of spatial scales, from local to global, and temporal scales, from days to multiple millennia [25]. Here we mainly consider the directional movement of species in response to environmental changes. The most common manifestation of such movement is that of range shifts (Figure 1) that might involve elevational, longitudinal or latitudinal changes in distribution [26]. For instance, pole-ward shifts of marine fish species have been documented in the oceans off eastern Australia and Japan, resulting in large changes in fish abundances [27, 28]. This shift in turn may have cascading effects on habitat by over-grazing dominant temperate macroalgae and facilitating the expansion of coral into temperate habitats [29]. Species may also shift their ranges within elevational gradients. In the rainforests of northern Australia, at least 28 bird species have been documented moving upslope as a result of climate warming and endemic possum species have extended their range upslope and/or declined at lower elevations [30]. Similar trends are seen elsewhere, for instance in the Alps [31] and the Sierra Nevada in California [32, 33], although species' responses vary considerably, with some species moving downslope or not moving at all.

2. Species that are moved by humans

Humans have been moving species from place to place throughout human history [34]. Indeed, the line between unassisted and human-assisted movement of species is often indistinct. For instance, populations of giant tortoises may have been emplaced on remote islands in the Indian Ocean by early Austronesian sailors [35], although this hypothesis remains controversial [36, 37]. Similarly, there is debate over whether lions and cheetahs dispersed to India themselves or were brought there via ancient trading routes by Indian royalty to populate hunting parks [38]. More generally, it may be hard to differentiate between climatically driven range shifts and those influenced by humans: for instance, a recent analysis of European vegetation change over the past 15,000 years discussed a likely role of human disturbance, use of fire, and direct dispersal in tree species' range changes in both Europe and North America [39]. Similar debates are underway over whether human-mediated invasions differ fundamentally from natural colonization events [40, 41], and how “native” and “non-native” species should be defined in an era where species are moving by themselves and are also being moved by humans [42, 43] .

The majority of current human interventions in ecosystems aim to maintain or modify the abundances of species – maintaining or increasing those that are valued and decreasing or removing those that are viewed as having disbenefits. As part of this aim, human migration and trade have resulted in the transport of a wide array of species considered beneficial for humans (including plants for food and fiber, horticultural species, livestock, pets, biocontrol agents). Most of the major crop and livestock species have been spread around the world by human transport and are maintained by cultivation or husbandry [44]. Humans have also transported species that are considered less desirable because of their impacts on production or native species and ecosystems. Invasive species include deliberate and inadvertent introductions [45]. Adverse effects of invasive species are well-documented, and efforts to eradicate or control problem species are ongoing in much of the world [46]. Predicting which species become invasive on being moved is complicated and requires knowledge of the species functional traits, the invasibility of the recipient ecosystem (often high for human-modified habitats) and the structure of the ecological network [47].

Increasingly, human movement of species is perceived as an important conservation tool. A spectrum of aims and approaches can be identified for conservation-related species translocation [48]. Translocation within the historic range is routine in management practice [49], aiming to improve the status of particular species (e.g., bolstering an existing population or reintroducing a species to formerly occupied areas), or to restore ecosystem functions and processes. Alternatively, species can be translocated to sites outside the previous range via assisted colonization, either to establish rescue populations in areas under reduced threat or to colonize new territory in anticipation of environmental shifts [50]. Other *ex situ* conservation efforts such as captive breeding and seed banking also depend initially on the transfer of species to zoos, gardens, seed vaults and the like.

Species may also be translocated to new areas as ecological surrogates for extinct species, with the aim of restoring particular functions or processes. For example, giant tortoises have been introduced to islands in the Mascarene and Galapagos Archipelagos, where endemic tortoises have gone extinct to reinstate missing ecological processes [51, 52]. A broader application, "rewilding" [53], has been the topic of considerable debate, particularly in relation to proposals to reinstate historic animal assemblages using fauna from other continents [54-56].

As an alternative to active translocation, many conservation plans include actions aimed at increasing landscape connectivity and hence increasing the opportunity for species to move by themselves. These initiatives range from localized actions such as the provision of highway overpasses to facilitate faunal movement across otherwise impermeable features through to continental-scale initiatives to maintain continuous stretches or stepping stones of habitat over large areas (including initiatives such as Yellowstone to Yukon and GondwanaLink) [57-59]

3. Species that move due to human-modified habitats or resources

An intermediate category includes species that move to take advantage of new habitat or altered resources created by human activity. This process has been ongoing for as long as humans have modified environments, with, for instance, large numbers of plant and fauna species associated with traditional agricultural and grazing systems. In addition the provision of water sources such as watering points in arid zones can result in the range expansion of many species [60]. Human-modified rangelands have also facilitated the cosmopolitan expansion of the cattle egret, a species that has naturally migrated to many parts of the world since the late 1800s [61]. Increasingly, an array of fauna species are moving into cities to take advantage of resources available there, particularly water, food and key structural habitat elements [62-64]. A dramatic example of the interplay between natural processes and human-created resources has been documented following this the Japanese tsunami in 2011, where debris from infrastructure transported hundreds of marine species across the Pacific [65].

Stayers

Although recent attention has centered on movement in response to climate change, much conservation activity focuses on maintaining species where they are now. Species may persist in a given place for a variety of reasons, and many management strategies focus on facilitating persistence of desirable species. In some cases, the identity and value of specific places centers on a single iconic species (e.g., Organ Pipe Cactus and Saguaro National Parks).

1. Species that stay put

Species that persist in existing habitats under environmental change do so for many reasons. Broad environmental tolerances may leave them unaffected by change. In the absence of evolutionary change, species can make any number of phenotypic adjustments to accommodate climate change *in situ*, including shifts in phenology, physiology, internal resource allocation, anatomy and morphology, and behavior [66, 67]. Many of these changes are species- and place-specific, and forecasting specific adjustments is difficult without extensive empirical observation (including fundamental natural history as well as monitoring). Ongoing phenological changes are receiving abundant attention, in part owing to emplacement of extensive monitoring networks [68]. Individualistic phenotypic responses among species may result in changes to ecosystem function [69] and to species interactions. As one example, divergent phenological shifts may yield mismatches between flowering and pollinator availability [70] and changes in resource availability for fauna [71].

In long-lived species, particularly sessile ones, adults may be unaffected by change, even though regeneration may be reduced or inhibited, potentially leading to eventual extinction [72]. In what amounts to an ‘inverse Allee effect’, incumbency may foster persistence in an increasingly unfavorable environment (e.g., via high propagule flux density, heavy shading, or soil biogeochemistry). Populations may also persist in local microrefugia that buffer broader environment changes [22-24]. On the other hand, they may simply be poor dispersers that are unable to move more than short distances or have extremely specialized habitat or resource requirements that restrict their movement. Populations of stayers may be subject to eventual extinction, owing to regeneration failure, adult-mortality events (e.g., severe disturbance), or continued environmental change that exceeds their capacity to adapt phenotypically (or evolutionarily – see below).

On the other hand, species that remain in place may benefit from the new circumstances. Extinction or departure of enemies or competitors may provide ecological release, and immigration of new species may offer new opportunities in the form of resources or habitats. Some species take advantage of or become dependent on these new resources, maintaining or increasing their populations by utilizing them (e.g. [73]). An important question is whether it is possible to predict how persisters might interact with new arrivals, a question that research from invasion biology may assist with answering.

Evidence is accumulating that many species populations have capacity to adjust to environmental change *in situ* via rapid evolution or phenotypic change [74-76]. Hybridization is a further response that may result in hybrid species that are better able to persist in changed conditions – for instance there is evidence for past and current hybridization between polar and brown bears as habitat distributions change [77, 78]. However, evolutionary capacity and rates are limited by genetic diversity, gene flow, effective population size, generation time, and selection pressure. Ultimately, the rate of local and regional climatic change may ultimately outstrip evolutionary adaptive capacity of populations, leading to their local extinction.

2. Species that stay with direct human assistance.

Human intervention to maintain plant and animal populations in place dates to the antiquity of plant cultivation and animal domestication, and has been part of conservation since its origins in timber management and game preservation. As societal values have evolved, conservation activities have expanded to include habitat manipulations and interventions aimed at maintaining populations of locally or universally threatened and endangered species, and of species of special concern. The latter group is diverse, including species that have particular values (e.g., iconic species that impart a distinct signature to a landscape, economically important species, species viewed as ecological keystones, species important for local cultural uses or practices), often expanded to incorporate the entire biodiversity of a place.

Conservation practices aimed at maintaining *in situ* populations are diverse, ranging from diffuse habitat manipulation and threat minimization to extreme intervention. As an example of the latter, old-growth hemlock trees (*Tsuga canadensis*) threatened by the exotic woolly adelgid are being kept alive along popular hiking trails in Great Smoky Mountains National Park by periodic treatment with a systematic insecticide (https://www.nps.gov/grsm/learn/nature/hemlock-woolly-adelgid.htm). A wide range of species are now considered to be conservation-reliant [79] – in other words, their persistence depends on human interventions of some sort. Growth in the number of conservation-reliant species and populations seems inevitable in the face of climatic change as well as other threats. Directional climate change may eventually render intervention efforts prohibitively costly or otherwise unsustainable in specific cases, leading to tradeoffs among conservation resources and, ultimately, excruciating decisions [80, 81].

Ex situ conservation is being increasingly applied in cases where *in situ* intervention is insufficient. But following such 'rescue', the species is functionally extinct in the habitat it once occupied. Moving species into captive breeding programs or seed vaults prevents actual extinction and can maintain populations in the hope of being able to reintroduce the species into the former habitat or new suitable areas [82]. However, captive breeding programs themselves have the potential to lead to micro-evolutionary changes, where the species adapts to the captive environment [83]. Environmental change, particularly climatic change, may ultimately render the original habitat environmentally unsuitable for reintroduction, so future conservation efforts may require relocation to newly suitable locales. Reviving species from material stored in vaults is a risky venture, and more generally, *ex situ* conservation efforts cannot hope to conserve species and species interactions as they are now.

3. Species that stay with indirect human assistance.

As with the movers, many species populations are able to persist because they can benefit from unintentional or diffuse human activities – activities that are not aimed specifically at management or conservation. A species may persist in a region by exploiting crops tended by humans, resources or functions provided by non-native species (shelter, food, pollination), or novel resources (artificial water sources, artificial reefs). In addition, direct human assistance can benefit particular species. Garden bird feeders, nesting boxes or backyard habitats are common in some countries [84], and these maintain or increase fauna populations, especially in cities, and can also affect associated insect prey [85].

Moved to action or moved to tears?

Some broad themes emerge from the discussion above. Firstly, some species will move in response to environmental change, and some will move faster than others. Some species that need to move cannot. Secondly, some species will stay. Some species will stay longer than others. New species mixtures will continually emerge (Boxes 1 and 2).

Indeed evidence is emerging that endemic species with narrow ranges that are unable to adapt or do not receive adequate interventive assistance may go extinct. For instance, the Bramble Cay melomys (*Melomys rubicola*), an Australian rodent, is thought to be the first species whose extinction can be related directly to current climate change as the primary agent [86, 87]. In the case of this and other recently extinct species, it is often hard to identify the causal factors involved, although it is clear that policy and management shortcomings play a part [88]. These are species that have not been helped to either stay put or to move. This situation can either move people to despair or spur them to take more effective actions. Human responses to changing biotas are important factors in determining what happens next (Box 3).

There is much to consider in making difficult management decisions on where and when to intervene (in moving or staying) and where to let species and places just be (Figure 3). Interventions can be directed at assisting species to move or stay, while indirect interventions can aim to reduce the need for direct assistance by tackling the big drivers of change, namely human population, ecosystem modification and exploitation, and climate change. While recognising the importance of indirect interventions, we focus here on direct interventions.

Obviously the categories of movers and stayers are not exclusive: any given species may exhibit more than one response and be subject to one or more human intervention(s) simultaneously. Species recovery plans often include multiple actions spanning the responses illustrated in Figure 3. However, it is important that the full portfolio of possible interventions is considered in order to maximise the likelihood of success by choosing species- and situation-appropriate interventions (or deciding not to intervene). The broader approach involves making decisions about where laissez-faire approaches can be adopted and where intervention is required.

Differential species responses and the formation of new assemblages may require a shift from individual species management and conservation of particular assemblages in a particular place (e.g., threatened ecological communities) to actions and goals that consider in a holistic manner how species will interact and how emerging assemblages will operate. Interventions based on moving species in or out of existing communities are likely to result in complex and potentially cascading effects [89-91]. While some of these effects can result in useful conservation outcomes, they also have potential to pose conservation conundrums. For instance, a threatened species moved to a new habitat could have negative impacts on other species resident there, or a threatened species could become dependent on what is otherwise considered a problem invasive species.

Hence, there are many potential advantages to be gained by framing interventions in a broader assemblage context, with win-win situations possible. How, practically, does one move from managing single-species to assemblage approaches? Much management and policy will still, of necessity, focus on single species but can take account of the multi-species context. Explicit recognition of the likelihood of altered species interactions needs to be part of every decision relating to individual species. Pre-empting unexpected and perverse outcomes by careful consideration of system dynamics and likely interactions needs to become a required part of conservation planning and decision-making. Anticipating conservation conundrums before they happen should be possible using these approaches. In addition, the management portfolio can be enlarged to include the adoption of options that include a mix of taxon-based and taxon-free (functional) approaches, including functional substitutions [1]. In a world of changing species distributions and assemblages, it will be increasingly important to understand how and why species move or stay and to deploy effective interventions that achieve desired conservation and restoration goals.

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Box 1. Moving and Staying on Dutch John Mountain.

Paleoecological records offer diverse examples of how species move or stay under environmental change. Among many examples of extreme movers is *Pinus banksiana.* The entire modern species range was under the Laurentide Ice Sheet at the last glacial maximum (LGM) ca. 20,000 years ago, and it has abandoned its extensive LGM range south of the ice margin [92]. Records at individual sites often display extensive ecological turnover, with movers coming and going and stayers persisting for various lengths of time [3]. The sequence of trees and shrubs recorded in a 20,000-year time-series of *Neotoma* (packrat) middens at Dutch John Mountain, in the central Rockies of the western USA [93], is characteristic (see the figure). Montane conifers, including *Pinus flexilis*, *Juniperus communis*, *Pseudotsuga menziesii*, and *Juniperus scopulorum* grew at the site at LGM, and all persisted through rapid warming and increasing moisture between 15,000 and 10,000 years ago. They were joined by other trees (*Picea pungens*) and shrubs (*Krasscheninnikovia lanata*, *Gutierrizia sarothrae*, *Juniperus horizontalis*, *Holodiscus dumosa*, *Philadephus microphyllus, Rhus trilobata, Cercocarpus* spp.). Many underwent local extinction during rapid warming and drying after 10,000 years ago. Most disappearances represent ‘moves’; populations of nearly all these species occur at higher elevations within 10-20 km of the site. *Juniperus osteosperma* immigrated from the south ca. 9000 years ago, and was joined by *Pinus ponderosa*; both have persisted ever since. *Pinus edulis* and *Ephedra viridis* colonized the site only 700 years ago [93][XX]. *Juniperus scopulorum*, *Krasscheninnikovia lanata*, and *Gutierrizia sarothrae* are long-term stayers; during their 20,000-year sojourn, they experienced a variety of environmental conditions as well as a wide variety of neighbors. *Juniperus horizontalis* occurred at the site as early as 14,000 years ago, persisting locally until ca. 6500 years ago. This species has been extirpated across the entire region; it was a stayer doomed to eventual extinction.

Box 2

It's a mixed up, muddled up, shook up world

Species rarely move into spaces not already occupied by other species. A given species may be invading new territory and staying put at the same time. In both cases it encounters new species. Hence new mixes of movers and stayers will increasingly occur, leading to novelty and increasing indeterminacy. Mixtures may be transient or stable, depending on strength of interactions that develop and rates of environmental change. Regardless, the result will be mixtures of species interacting in novel ways. The populations of species that stay may either increase, decrease or undergo no net change, depending on whether they benefit from the new environment, exploit new resources, lose existing resources, or face competition or consumption from incoming species. Thus, new mixtures could range from simple addition or deletion of a species or two to emergence of entirely new assemblages. Paleoecological records contain many examples of community transitions where some species disappear, some new ones invade, and some incumbents stay in place (Box 1). These changes may aggregate over time to drive complete species turnover [2].

Understanding species and community dynamics in an increasingly modified world will require research that focuses on a range of questions, including:

1. How will 'old' communities function in new places and under new environments?
2. How will novel assemblages function in all the places they arise?
3. How will combinations of stayers and immigrants interact in communities, and how will this affect overall ecosystem functioning (and hence ecosystem services)?
4. Will mixes of native immigrants and stayers behave differently or more predictably than those comprising native stayers and non-native (transcontinental) immigrants?
5. Will mixes of native stayers and non-native immigrants behave differently from mixes of non-native stayers and native immigrants?

6. When species immigrate to a site, what challenges (competition, consumption, habitat alteration) and opportunities (new resources, new mutualists) do they pose for the stayers?

Paleoecological records and invasive species research are obvious places to start answering these questions [2, 91, 94], but there is an opportunity to observe and model current and future dynamics in a more comprehensive way.

BOX 3

People's responses to changing nature

Human perceptions of nature vary greatly depending on geographic, socio-economic, religious, and many other influences. Concomitantly, human perceptions of changes in nature are also likely to be highly variable. It is likely that many people will neither notice nor care about the species and community dynamics described in this paper. Widespread apathy and a lack of awareness are major obstacles to the achievement of conservation goals and may result in many more unplanned and unexpected biotic changes than would be the case if there was widespread public interest in, and commitment to, conservation and restoration.

On the other hand, there are sections of the human community that are well connected to nature and recognise the importance of maintaining functioning ecosystems and conserving species and assemblages. Indigenous cultures that have been present over centuries or millennia have inevitably experienced ongoing environmental change, and place-based traditional ecological knowledge offers an important perspective of people's actual and potential responses to ecological change. While traditional ecological knowledge can help cultures adapt to gradual change, research suggests this knowledge is rarely adequate for coping with sudden or widespread changes [95]. As one example, indigenous people in Northern Australia express great concern towards recent human-mediated changes including native species declines associated with mining development, tourism and climate change [96].

The redistribution of species and formation of new biotic assemblages has profound implications for ecosystem functioning and human well-being [9], which depends not just on the material goods and services people derive from nature but also cultural identity [97]. Sense of place and lived experiences of places and landscapes help to define cultural identity and to motivate place-based conservation [98]. Places are defined by their physical location, ‘materiality’ including nature, and meaning to people [99]. Modern cities offer some insight into the ways people respond to ecological change happening on their doorstep, and provide some evidence that people can attach to new assemblages in old places [100]. The future success of place-based conservation efforts will be determined in part by the willingness of people to develop new meanings for places as they change.

Figure Legends

Figure 1. Species ranges can change in several ways, including directional shift in which the range contracts at one edge and expands at the other, contraction to refugia, and fragmentation caused by changed land use such as urban and agricultural development. Range expansion at one edge without contraction at the other is also possible.

Figure 2.

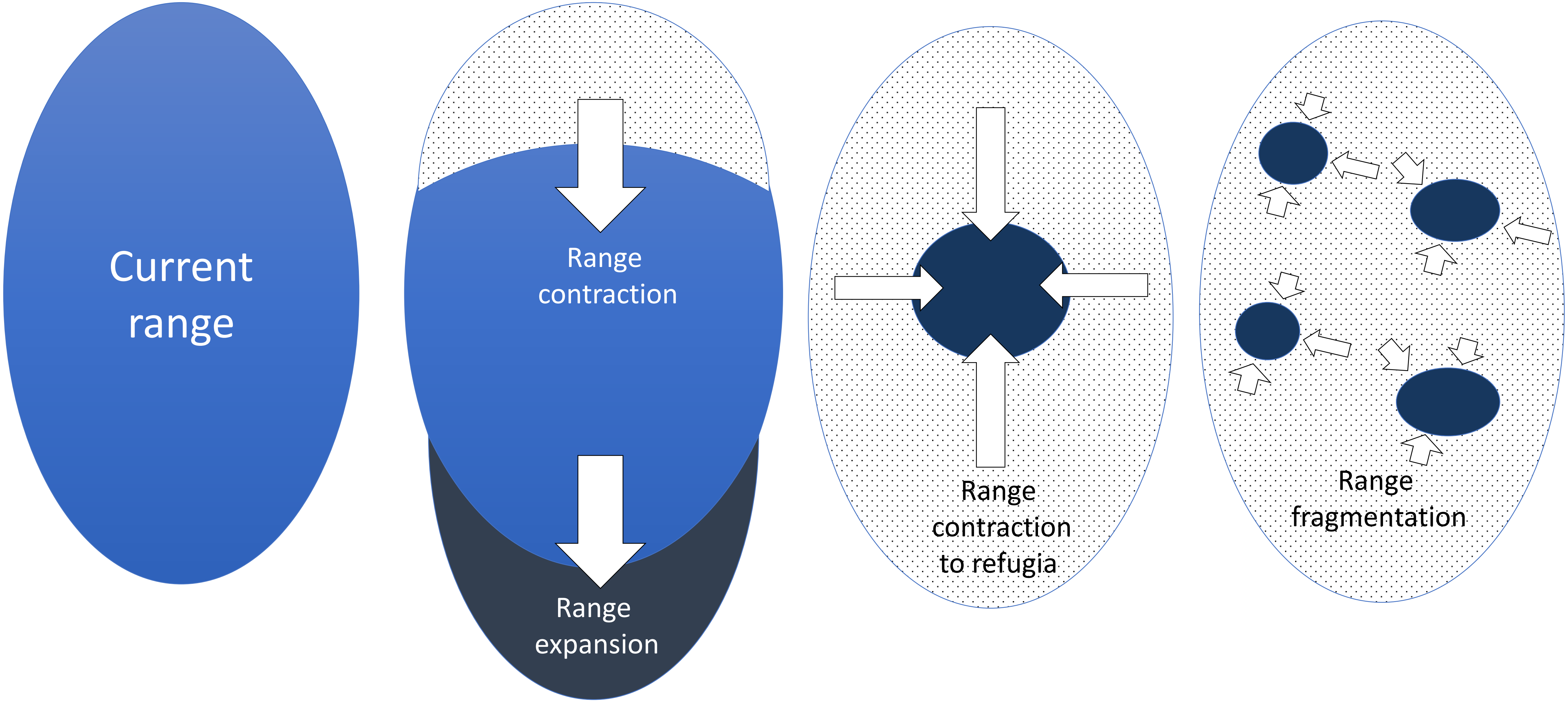
Examples of the methods of movement that species can display in response to environmental and human-mediated changes. Species can expand or contract their ranges in both within and outside of their existing distributions. Humans have a long history of directly contributing to species movement in multiple ways, from the deliberate movement of species to the accidental, and via long-term management of landscapes. Humans, through habitat modification, the creation of novel environments, such as cities and agricultural landscapes and the provision of novel resources that facilitate movement, can influence movement of species. These examples illustrate three groups of species movement: i) species that move themselves (blue) ii) species that are moved by humans (orange) and iii) species that move themselves because of humans (green). Each box represents a specific example, with arrows (where appropriate) indicating the direction of movement. The human figures indicate the original location of a species prior to human movement.

Figure 3. Conceptual scheme showing potential response capacities of populations or species to environmental change, and potential conservation measures that might (or might not) be taken. Success of 'stayers' (top row) will depend on their *persistence capacity* relative to the rate and magnitude of environmental change. Persistence capacity will depend on a variety of factors, including phenotypic plasticity, evolutionary potential, genetic diversity, proximity of source populations for extinction 'rescue', and pressure from old and new competitors and consumers. 'Stayers' range from populations that benefit from the existing circumstances (left) to populations

under dire threat of extinction (right). *Migration capacity*, which addresses the ability of 'movers' (second row) to emigrate to more suitable habitat elsewhere, or to immigrate to a particular site to exploit new opportunities, depends on life-history attributes (dispersal, establishment, population growth-rates) relative to rate and magnitude of environmental change and to local factors (disturbance, competition, consumers). Migration capacity ranges from highly effective to nil. Both stayers and movers that are on the left-hand side of the diagram at one time and place may be on the right-hand side at others. For example, if an environmental change at a particular site ultimately spans the entire environmental niche breadth of a species, a population initially at severe risk of extinction would expand and ultimately prosper as the environment passed through its optimum, and then decline and become vulnerable to extinction again as the environment approached the trailing edge of the species niche. Conservationists can 'let it be' in situations on the left-hand side of the diagram, but increasing levels of intervention may be required towards the right, from moderate 'assists' to massive intervention. The boundary between 'intervention ecology' and 'laissez-faire ecology' is fuzzy, depending on perceptions of risk (vulnerability X consequences) and societal capacity (management resources, available technology).

BOX 1 Figure 1 Occurrence of selected tree and shrub species in a 20,000-year time-series of woodrat (*Neotoma*) middens from Dutch John Mountain in northeastern Utah, USA. Dots denote presence of the species in a midden of a particular age. Modified from [93].

Figure 1


Current range
Range contraction
Range expansion
Range contraction to refugia
Range fragmentation

Hobbs et al Figure 2

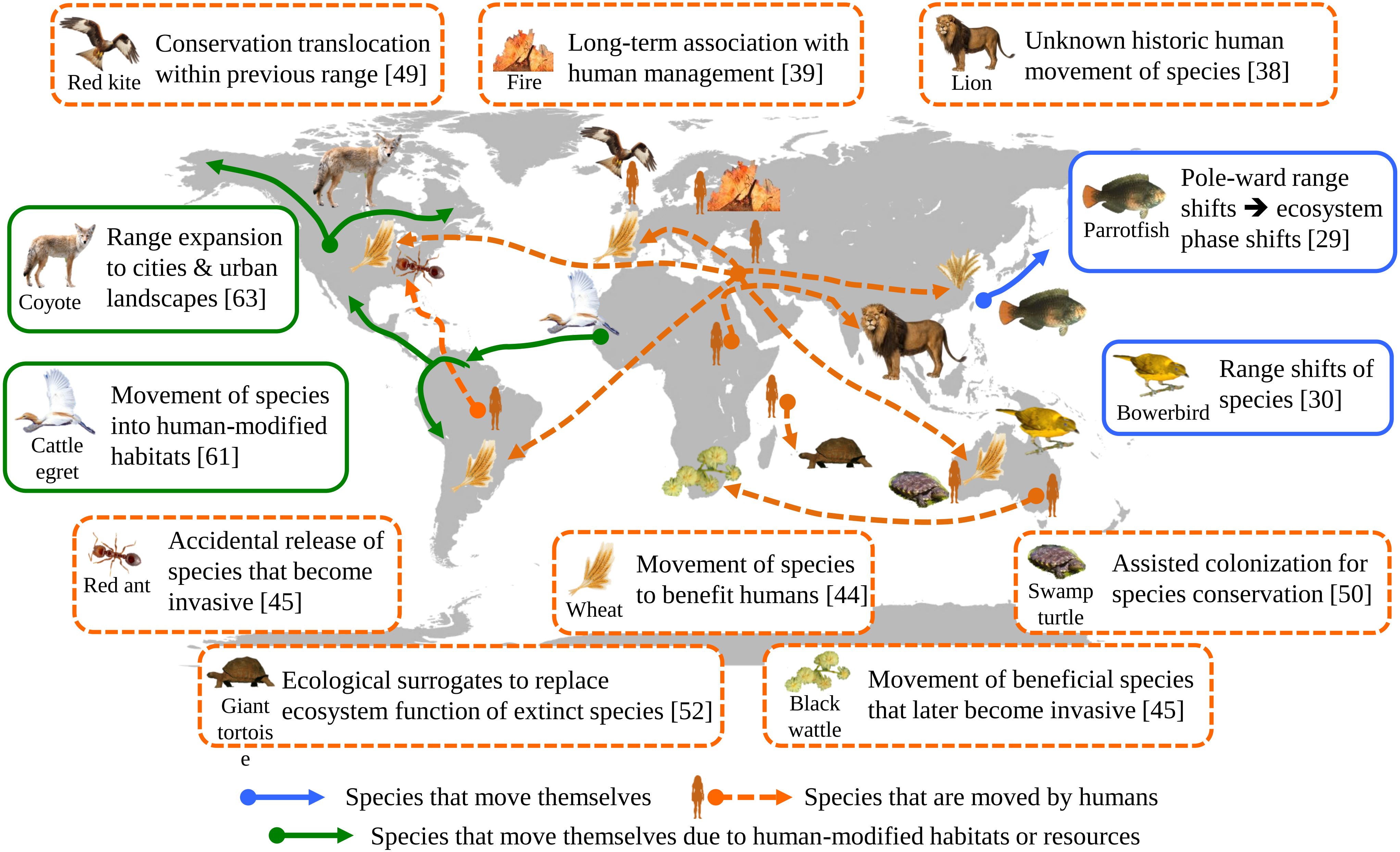
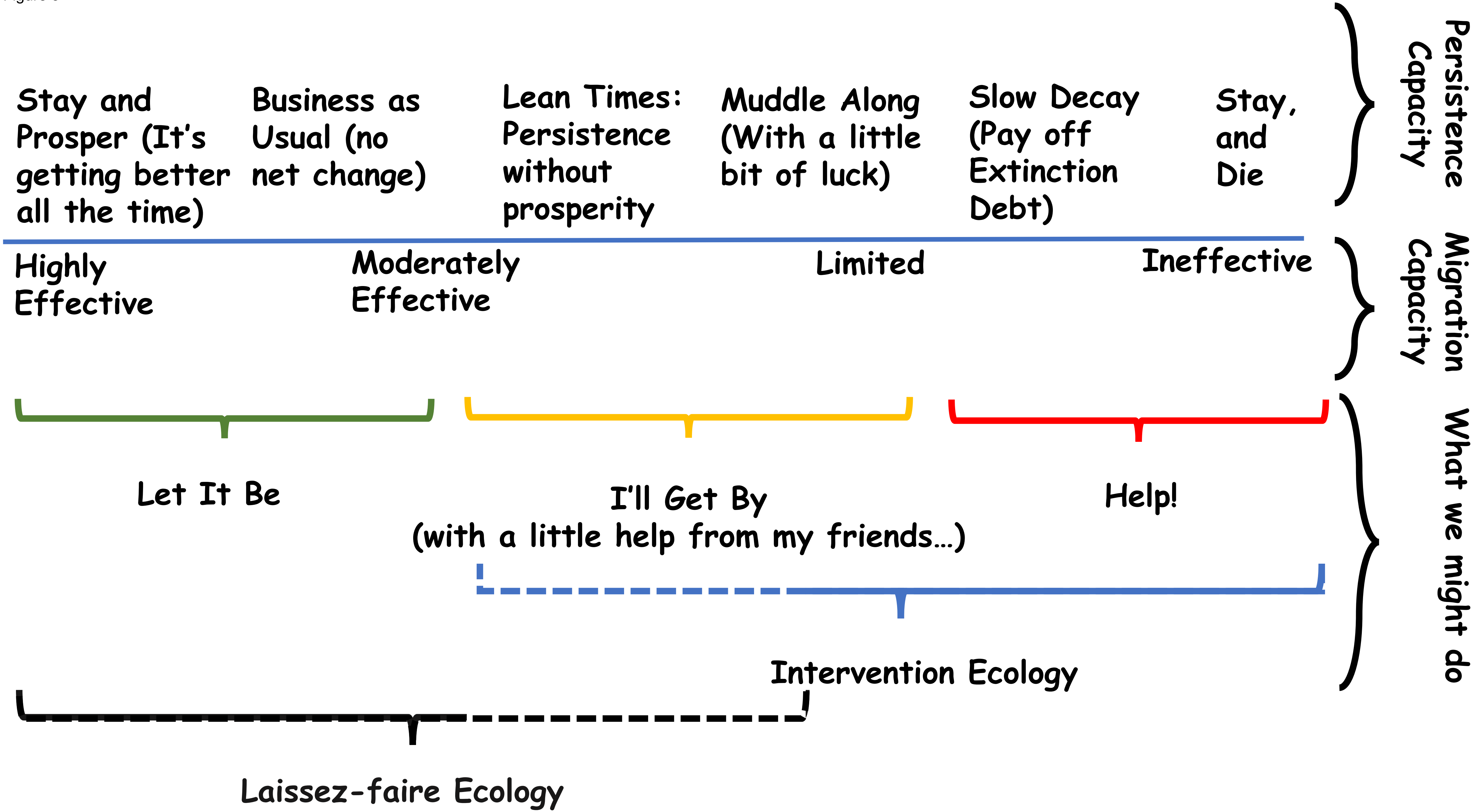
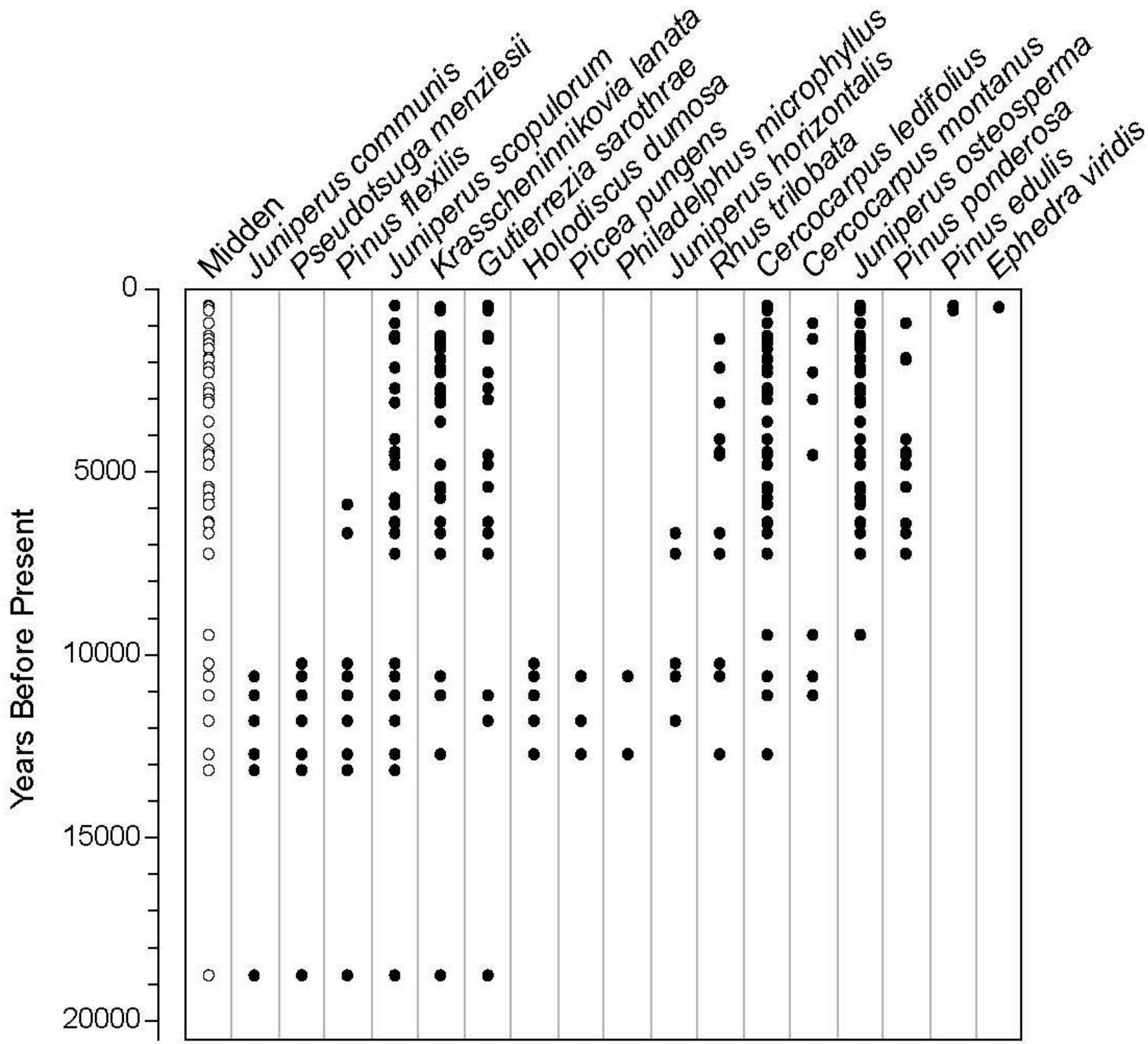


Figure 3


Stay and Prosper (It's getting better all the time)
Business as Usual (no net change)
Lean Times: Persistence without prosperity
Muddle Along (With a little bit of luck)
Slow Decay (Pay off Extinction Debt)
Stay, and Die
Persistence Capacity
Highly Effective
Moderately Effective
Limited
Ineffective
Migration Capacity
Let It Be
I'll Get By
(with a little help from my friends...)
Help!
Intervention Ecology
Laissez-faire Ecology
What we might do

Hobbs et al Box 1 Figure 1



Trends

How species will respond to ongoing climate and other change is of increasing concern.

Most attention is given to how species move or are moved, but many species stay.

Understanding the dynamics of new species combinations is essential for successful conservation in a changing climate.

Outstanding questions

How will combinations of mover and stayer species interact, and how will this affect ecosystem functioning and conservation outcomes?

How can place- and species-based conservation strategies be modified to improve conservation outcomes in a rapidly changing world?

Can the ability of species to move and/or persist be adequately assessed to allow the development of effective interventions?