1 **Movers and stayers: novel assemblages in changing environments**

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For review only

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

41 normal ranges. This deliberate transport includes transport of potentially invasive species [10, 11]
42 and assisted migration of species at risk [12-14].

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

49 Species assemblages under environmental change thus comprise mixes of stayers (some of
50 which are doomed to eventual extinction and some which will persist), and movers, which invade
51 and expand at different rates. The transient dynamics of current-day ecosystems and assemblages
52 that result from these species mixes have received relatively little attention [7]. Species distribution
53 modelling has focused almost exclusively on single species, and inclusion of mechanistic
54 consideration of how species interactions will affect outcomes remains challenging [16-18]. Where
55 species assemblages are considered, indications are that individualistic species responses to climate
56 and other changes will result in assemblages of varying degrees of novelty, ranging from not novel
57 (e.g., similar communities already occur elsewhere) to completely novel species combinations (e.g.
58 [19]).

59 In this paper we provide an overview of the various categories of species from the
60 perspective of whether they are movers or stayers in a changing world, and we consider what this
61 means for management and conservation. Although species and community dynamism are implicit
62 in many aspects of ecology, including metapopulation biology, island biogeography and the like,
63 current work on dynamics in the face of global change tends to focus on particular aspects of this
64 dynamism. Different modes of movement (or lack thereof) are seldom considered together as a
65 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],

118 and how “native” and “non-native” species should be defined in an era where species are moving by
119 themselves and are also being moved by humans [42, 43] .

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

133 Increasingly, human movement of species is perceived as an important conservation tool. A
134 spectrum of aims and approaches can be identified for conservation-related species translocation
135 [48]. Translocation within the historic range is routine in management practice [49], aiming to
136 improve the status of particular species (e.g., bolstering an existing population or reintroducing a
137 species to formerly occupied areas), or to restore ecosystem functions and processes. Alternatively,
138 species can be translocated to sites outside the previous range via assisted colonization, either to
139 establish rescue populations in areas under reduced threat or to colonize new territory in
140 anticipation of environmental shifts [50]. Other *ex situ* conservation efforts such as captive
141 breeding and seed banking also depend initially on the transfer of species to zoos, gardens, seed
142 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].

169 **Stayers**

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

175 *1. Species that stay put*

176 Species that persist in existing habitats under environmental change do so for many reasons. Broad
 177 environmental tolerances may leave them unaffected by change. In the absence of evolutionary
 178 change, species can make any number of phenotypic adjustments to accommodate climate change
 179 *in situ*, including shifts in phenology, physiology, internal resource allocation, anatomy and
 180 morphology, and behavior [66, 67]. Many of these changes are species- and place-specific, and
 181 forecasting specific adjustments is difficult without extensive empirical observation (including
 182 fundamental natural history as well as monitoring). Ongoing phenological changes are receiving
 183 abundant attention, in part owing to emplacement of extensive monitoring networks [68].
 184 Individualistic phenotypic responses among species may result in changes to ecosystem function
 185 [69] and to species interactions. As one example, divergent phenological shifts may yield
 186 mismatches between flowering and pollinator availability [70] and changes in resource availability
 187 for fauna [71].

188 In long-lived species, particularly sessile ones, adults may be unaffected by change, even
 189 though regeneration may be reduced or inhibited, potentially leading to eventual extinction [72]. In
 190 what amounts to an ‘inverse Allee effect’, incumbency may foster persistence in an increasingly
 191 unfavorable environment (e.g., via high propagule flux density, heavy shading, or soil
 192 biogeochemistry). Populations may also persist in local microrefugia that buffer broader
 193 environment changes [22-24]. On the other hand, they may simply be poor dispersers that are
 194 unable to move more than short distances or have extremely specialized habitat or resource

195 requirements that restrict their movement. Populations of stayers may be subject to eventual
 196 extinction, owing to regeneration failure, adult-mortality events (e.g., severe disturbance), or
 197 continued environmental change that exceeds their capacity to adapt phenotypically (or
 198 evolutionarily – see below).

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

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

214 2. *Species that stay with direct human assistance.*

215 Human intervention to maintain plant and animal populations in place dates to the antiquity
 216 of plant cultivation and animal domestication, and has been part of conservation since its origins in
 217 timber management and game preservation. As societal values have evolved, conservation activities
 218 have expanded to include habitat manipulations and interventions aimed at maintaining populations
 219 of locally or universally threatened and endangered species, and of species of special concern. The
 220 latter group is diverse, including species that have particular values (e.g., iconic species that impart

221 a distinct signature to a landscape, economically important species, species viewed as ecological
 222 keystones, species important for local cultural uses or practices), often expanded to incorporate the
 223 entire biodiversity of a place.

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

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

246 3. *Species that stay with indirect human assistance.*

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

255

256 **Moved to action or moved to tears?**

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

261

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

271

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

278

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

286

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

296

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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References

- 1 Barnosky, A.D., *et al.* (2017) Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* 355
- 2 Jackson, S.T. and Blois, J.L. (2015) Community ecology in a changing environment: Perspectives from the Quaternary. *Proceedings of the National Academy of Sciences* 112, 4915-4921

- 323 3 Jackson, S.T. (2006) Vegetation, environment, and time: the origination and termination of
 324 ecosystems. *J. Veg. Sci.* 17, 549-557
- 325 4 Steffen, W., *et al.* (2011) The Anthropocene: conceptual and historical perspectives.
 326 *Philosophical Transactions: Mathematical, Physical and Engineering Sciences* 369, 842-867
- 327 5 Ellis, E.C. (2015) Ecology in an anthropogenic biosphere. *Ecol. Monogr.* 85, 287–331
- 328 6 Lawler, J.J., *et al.* (2015) The theory behind, and the challenges of, conserving nature's stage in a
 329 time of rapid change. *Conserv. Biol.* 29, 618-629
- 330 7 Magurran, A.E. (2016) How ecosystems change. *Science* 351, 448-449
- 331 8 Pandolfi, J.M. and Lovelock, C.E. (2014) Novelty trumps loss in global biodiversity. *Science* 344,
 332 266-267
- 333 9 Pecl, G.T., *et al.* (2017) Biodiversity redistribution under climate change: Impacts on ecosystems
 334 and human well-being. *Science* 355
- 335 10 Lockwood, J.L., *et al.* (2013) *Invasion Ecology 2nd Edition*. Wiley-Blackwell
- 336 11 Simberloff, D. (2013) *Invasive Species: What Everyone Needs to Know*. Oxford University Press
- 337 12 Richardson, D.M., *et al.* (2009) Multidimensional evaluation of managed relocation.
 338 *Proceedings of the National Academy of Sciences* 106, 9721-9724
- 339 13 Sansilvestri, R., *et al.* (2015) Reconstructing a deconstructed concept: Policy tools for
 340 implementing assisted migration for species and ecosystem management. *Environmental Science &*
 341 *Policy* 51, 192-201
- 342 14 Hällfors, M.H., *et al.* (2017) Quantifying the need and potential of assisted migration. *Biol.*
 343 *Conserv.* 205, 34-41
- 344 15 Jackson, S.T. and Sax, D.F. (2010) Balancing biodiversity in a changing environment: extinction
 345 debt, immigration credit and species turnover. *Trends in Ecology & Evolution* 25, 153-160
- 346 16 Copenhaver-Parry, P.E., *et al.* (2016) Do community-level models account for the effects of
 347 biotic interactions? A comparison of community-level and species distribution modeling of Rocky
 348 Mountain conifers. *Plant Ecology* 217, 533-547

- 349 17 Singer, A., *et al.* (2016) Community dynamics under environmental change: How can next
350 generation mechanistic models improve projections of species distributions? *Ecological Modelling*
351 326, 63-74
- 352 18 Thuiller, W., *et al.* (2015) From species distributions to meta-communities. *Ecology Letters* 18,
353 1321-1328
- 354 19 Stralberg, D., *et al.* (2009) Re-shuffling of species with climate disruption: A no-analog future
355 for California birds? *PLoS ONE* 4, e6825
- 356 20 Ceballos, G., *et al.* (2017) Biological annihilation via the ongoing sixth mass extinction signaled
357 by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*
- 358 21 Ettinger, A.K. and HilleRisLambers, J. (2013) Climate isn't everything: Competitive interactions
359 and variation by life stage will also affect range shifts in a warming world. *Am. J. Bot.* 100, 1344-
360 1355
- 361 22 Keppel, G., *et al.* (2012) Refugia: identifying and understanding safe havens for biodiversity
362 under climate change. *Global Ecology and Biogeography* 21, 393-404
- 363 23 Morelli, T.L., *et al.* (2016) Managing climate change refugia for climate adaptation. *PLOS One*
364 11(8), e0159909
- 365 24 McLaughlin, B.C., *et al.* (2017) Hydrologic refugia, plants, and climate change. *Global Change*
366 *Biology* 23, 2941-2961
- 367 25 Wilson, J.R.U., *et al.* (2009) Something in the way you move: dispersal pathways affect invasion
368 success. *Trends in Ecology & Evolution* 24, 136-144
- 369 26 Lenoir, J. and Svenning, J.C. (2015) Climate-related range shifts – a global multidimensional
370 synthesis and new research directions. *Ecography* 38, 15-28
- 371 27 Johnson, C.R., *et al.* (2011) Climate change cascades: Shifts in oceanography, species' ranges
372 and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine*
373 *Biology and Ecology* 400, 17-32

- 374 28 Last, P.R., *et al.* (2011) Long-term shifts in abundance and distribution of a temperate fish fauna:
 375 a response to climate change and fishing practices. *Global Ecology and Biogeography* 20, 58-72
- 376 29 Vergés, A., *et al.* (2014) The tropicalization of temperate marine ecosystems: climate-mediated
 377 changes in herbivory and community phase shifts. *Proceedings of the Royal Society B: Biological*
 378 *Sciences* 281
- 379 30 Williams, S.E., *et al.* (2016) *Ancient, endemic, rare and threatened vertebrates of the Wet*
 380 *Tropics. State of the Wet Tropics Report.* Wet Tropics Management Authority
- 381 31 Büntgen, U., *et al.* (2017) Elevational range shifts in four mountain ungulate species from the
 382 Swiss Alps. *Ecosphere* 8, e01761
- 383 32 Rapacciuolo, G., *et al.* (2014) Beyond a warming fingerprint: individualistic biogeographic
 384 responses to heterogeneous climate change in California. *Global Change Biology* 20, 2841-2855
- 385 33 Rowe, K.C., *et al.* (2015) Spatially heterogeneous impact of climate change on small mammals
 386 of montane California. *Proceedings of the Royal Society B: Biological Sciences* 282
- 387 34 Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era
 388 of globalization. *J. Appl. Ecol.* 46, 10-18
- 389 35 Wilmé, L., *et al.* (2017) Human translocation as an alternative hypothesis to explain the presence
 390 of giant tortoises on remote islands in the south-western Indian Ocean. *J. Biogeog.* 44, 1-7
- 391 36 Hansen, D.M., *et al.* (2016) Origins of endemic island tortoises in the western Indian Ocean: a
 392 critique of the human-translocation hypothesis. *J. Biogeog.* 44, 1430–1435
- 393 37 Cheke, A.S., *et al.* (2016) Giant tortoises spread to western Indian Ocean islands by sea drift in
 394 pre-Holocene times, not by later human agency – response to Wilmé *et al.* (2016a). *J. Biogeog.* 44,
 395 1426–1429
- 396 38 Thapar, V., *et al.* (2013) *Exotic Aliens: The Lion and Cheetah in India.* Aleph Book Company
- 397 39 Giesecke, T., *et al.* (2017) Patterns and dynamics of European vegetation change over the last
 398 15,000 years. *J. Biogeog.* 44, 1441–1456

- 400 40 Wilson, J.R.U., *et al.* (2016) Biological invasions and natural colonisations are different – the
401 need for invasion science *NeoBiota* 31, 87-98
- 402 41 Hoffmann, B.D. and Courchamp, F. (2016) Biological invasions and natural colonisations: are
403 they that different? . *NeoBiota* 29, 1-14
- 404 42 Marinelli, J. (2016) As World warms, how do we decide when a plant is native? *Environment*
405 360
406 http://e360.yale.edu/feature/how_do_we_decide_when_a_plant_is_native_climate_change/2984/
- 407 43 Gilroy, J.J., *et al.* (2016) Seeking international agreement on what it means to be “native”.
408 *Conservation Letters* 10, 238-247
- 409 44 Leff, B., *et al.* (2004) Geographic distribution of major crops across the world. *Global*
410 *Biogeochemical Cycles* 18, GB1009
- 411 45 Global Invasive Species Database (2017) Accessed from <http://www.iucngisd.org/gisd> July
412 2017
- 413 46 Simberloff, D. (2014) Biological invasions: What's worth fighting and what can be won?
414 *Ecological Engineering* 65, 112-121
- 415 47 Hui, C., *et al.* (2016) Defining invasiveness and invasibility in ecological networks. *Biological*
416 *Invasions* 18, 971-983
- 417 48 Seddon, P.J., *et al.* (2014) Reversing defaunation: Restoring species in a changing world.
418 *Science* 345, 406-412
- 419 49 Carter, I., *et al.* (2017) The role of animal translocations in conserving British wildlife: an
420 overview of recent work and prospects for the future. *EcoHealth* 14, 7-15
- 421 50 Mitchell, N., *et al.* (2013) Linking eco-energetics and eco-hydrology to select sites for the
422 assisted colonization of Australia’s rarest reptile. *Biology* 2, 1-25
- 423 51 Hunter, E.A., *et al.* (2013) Equivalency of Galápagos giant tortoises used as ecological
424 replacement species to restore ecosystem functions. *Conserv. Biol.* 27, 701-709

- 425 52 Griffiths, C.J., *et al.* (2010) The use of extant non-indigenous tortoises as a restoration tool to
 426 replace extinct ecosystem engineers. *Restoration Ecology* 18, 1-7
- 427 53 Svenning, J.-C., *et al.* (2016) Science for a wilder Anthropocene: Synthesis and future directions
 428 for trophic rewilding research. *Proceedings of the National Academy of Sciences* 113, 898-906
- 429 54 Donlan, C.J., *et al.* (2006) Pleistocene rewilding: An optimistic agenda for twenty-first century
 430 conservation. *Am. Nat.* 168, 661-681
- 431 55 Oliveira-Santos, L.G.R. and Fernandez, F.A.S. (2010) Pleistocene Rewilding, Frankenstein
 432 Ecosystems, and an Alternative Conservation Agenda. *Conserv. Biol.* 24, 4-5
- 433 56 Rubenstein, D.R. and Rubenstein, D.I. (2016) From Pleistocene to trophic rewilding: A wolf in
 434 sheep's clothing. *Proceedings of the National Academy of Sciences* 113, E1
- 435 57 Belote, R.T., *et al.* (2017) Wild, connected, and diverse: building a more resilient system of
 436 protected areas. *Ecol. Appl.* 27, 1050-1056
- 437 58 Bradby, K., *et al.* (2016) Gondwana Link: connecting people, landscapes, and livelihoods across
 438 southwestern Australia. *Restoration Ecology* 24, 827-835
- 439 59 Rappaport, D.I., *et al.* (2015) A landscape triage approach: combining spatial and temporal
 440 dynamics to prioritize restoration and conservation. *J. Appl. Ecol.* 52, 590-601
- 441 60 James, C.D., *et al.* (1999) Provision of watering points in the Australian arid zone: a review of
 442 effects on biota. *J. Arid. Env.* 41, 87-121
- 443 61 Massa, C., *et al.* (2014) On how cattle egret (*Bubulcus ibis*) spread to the Americas:
 444 meteorological tools to assess probable colonization trajectories. *International Journal of*
 445 *Biometeorology* 58, 1879 – 1891
- 446 62 Donovan, T. (2015) *Feral cities: adventures with animals in the urban jungle*. Chicago Review
 447 Press
- 448 63 Williams, N.S.G., *et al.* (2006) Range expansion due to urbanization: Increased food resources
 449 attract Grey-headed Flying-foxes (*Pteropus poliocephalus*) to Melbourne. *Austral Ecology* 31, 190-
 450 198

- 451 64 Johnstone, R.E., *et al.* (2017) The distribution, status, movements and diet of the Forest Red-
 452 tailed Black Cockatoo in the south-west with emphasis on the greater Perth Region, Western
 453 Australia. *West. Aust. Nat.* 30, 193-219
- 454 65 Carlton, J.T., *et al.* (2017) Tsunami-driven rafting: Transoceanic species dispersal and
 455 implications for marine biogeography. *Science* 357, 1402-1406
- 456 66 Dawson, T.P., *et al.* (2011) Beyond predictions: Biodiversity conservation in a changing climate.
 457 *Science* 332, 53-58
- 458 67 Beever, E.A., *et al.* (2017) Behavioral flexibility as a mechanism for coping with climate
 459 change. *Frontiers in Ecology and the Environment* 15, 299-308
- 460 68 Primack, R.B. and Miller-Rushing, A.J. (2011) Broadening the study of phenology and climate
 461 change. *New Phytol.* 191, 307-309
- 462 69 Groffman, P.M., *et al.* (2012) Long-term integrated studies show complex and surprising effects
 463 of climate change in the northern hardwood forest. *BioScience* 62, 1056-1066
- 464 70 Donoso, I., *et al.* (2016) Phenological asynchrony in plant–butterfly interactions associated with
 465 climate: a community-wide perspective. *Oikos* 125, 1434-1444
- 466 71 Butt, N., *et al.* (2015) Cascading effects of climate extremes on vertebrate fauna through changes
 467 to low-latitude tree flowering and fruiting phenology. *Global Change Biology* 21, 3267-3277
- 468 72 Jackson, S.T., *et al.* (2009) Ecology and the ratchet of events: Climate variability, niche
 469 dimensions, and species distributions. *Proceedings of the National Academy of Sciences* 106,
 470 19685-19692
- 471 73 Raynor, E.J., *et al.* (2017) Effects of Tamarix removal on the community dynamics of riparian
 472 birds in a semiarid grassland. *Restoration Ecology* 28, 778-787
- 473 74 Hoffmann, A.A. and Sgro, C.M. (2011) Climate change and evolutionary adaptation. *Nature*
 474 470, 479-485
- 475 75 Rey, O., *et al.* (2016) Adaptation to global change: A transposable element–epigenetics
 476 perspective. *Trends in Ecology & Evolution* 31, 514-526

- 477 76 Flores-Moreno, H., *et al.* (2015) In the beginning: phenotypic change in three invasive species
478 through their first two centuries since introduction. *Biological Invasions* 17, 1215-1225
- 479 77 Miller, W., *et al.* (2012) Polar and brown bear genomes reveal ancient admixture and
480 demographic footprints of past climate change. *Proceedings of the National Academy of Sciences*
481 109, E2382–E2390
- 482 78 Peacock, E., *et al.* (2015) Implications of the circumpolar genetic structure of polar bears for
483 their conservation in a rapidly warming Arctic. *PLoS ONE* 10, e112021
- 484 79 Scott, J.M., *et al.* (2010) Conservation-reliant species and the future of conservation.
485 *Conservation Letters* 3, 91-97
- 486 80 Wiens, J.A. and Hobbs, R.J. (2015) Integrating conservation and restoration in a changing world.
487 *BioScience* 65, 302-312
- 488 81 Wilson, K.A. and Law, E.A. (2016) Ethics of conservation triage. *Frontiers of Ecology and*
489 *Evolution* 4, 12. doi: 10.3389/fevo.2016.00112
- 490 82 Canessa, S., *et al.* (2016) Planning for ex situ conservation in the face of uncertainty. *Conserv.*
491 *Biol.* 30, 599-609
- 492 83 O'Connor, M.R. (2015) *Resurrection science: Conservation, de-Extinction and the precarious*
493 *future of wild things*. St Martin's Press
- 494 84 Horn, D.J., *et al.* (2014) Seed and feeder use by birds in the United States and Canada. *Wildl.*
495 *Soc. Bull.* 38, 18-25
- 496 85 Orros, M.E. and Fellowes, M.D.E. (2012) Supplementary feeding of wild birds indirectly affects
497 the local abundance of arthropod prey. *Basic and Applied Ecology* 13, 286-293
- 498 86 Watson, J. (2016) Bring climate change back from the future. *Nature* 534, 437
- 499 87 Fulton, G.R. (2017) The Bramble Cay melomys: the first mammalian extinction due to human-
500 induced climate change. *Pac. Conserv. Biol.* 23, 1-3

- 88 Woinarski, J.C.Z., *et al.* (2017) The contribution of policy, law, management, research, and advocacy failings to the recent extinctions of three Australian vertebrate species. *Conserv. Biol.* 31, 13-23
- 89 Ruscoe, W.A., *et al.* (2011) Unexpected consequences of control: competitive vs. predator release in a four-species assemblage of invasive mammals. *Ecology Letters* 14, 1035-1042
- 90 Wallach, A.D., *et al.* (2015) Novel trophic cascades: apex predators enable coexistence. *Trends in Ecology & Evolution* 30, 146-153
- 91 Zavaleta, E.S., *et al.* (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* 16, 454-459
- 92 Jackson, S.T., *et al.* (2000) Vegetation and environment in unglaciated eastern North America during the last glacial maximum. *Quaternary Science Reviews* 19, 489-508
- 93 Jackson, S.T., *et al.* (2005) A 40,000-year woodrat-midden record of vegetational and biogeographic dynamics in northeastern Utah. *J. Biogeog.* 32, 1085-1106
- 94 Blois, J.L., *et al.* (2013) Climate change and the past, present, and future of biotic interactions. *Science* 341, 499-504
- 95 Adger, W.N., *et al.* (2012) Cultural dimensions of climate change impacts and adaptation. *Nature Climate Change* 3, 112
- 96 Petheram, L., *et al.* (2010) "Strange changes": Indigenous perspectives of climate change and adaptation in NE Arnhem Land (Australia). *Global Environmental Change* 20, 681-692
- 97 Adger, W.N., *et al.* (2011) This must be the place: Underrepresentation of identity and meaning in climate change decision-making. *Global Environmental Politics* 11, 1-25
- 98 Brandenburg, A.M. and Carroll, M.S. (1995) Your place or mine?: The effect of place creation on environmental values and landscape meanings. *Society and Natural Resources* 8, 381-398
- 99 Stewart, W.P., *et al.*, eds (2013) *Place-Based Conservation: Perspectives from the Social Sciences* Springer
- 100 Marris, E. (2011) *Rambunctious Garden: Saving Nature in a Post-Wild World*. Bloomsbury

527 **Box 1. Moving and Staying on Dutch John Mountain.**

528 Paleocological records offer diverse examples of how species move or stay under environmental
 529 change. Among many examples of extreme movers is *Pinus banksiana*. The entire modern species
 530 range was under the Laurentide Ice Sheet at the last glacial maximum (LGM) ca. 20,000 years ago,
 531 and it has abandoned its extensive LGM range south of the ice margin [92]. Records at individual
 532 sites often display extensive ecological turnover, with movers coming and going and stayers
 533 persisting for various lengths of time [3]. The sequence of trees and shrubs recorded in a 20,000-
 534 year time-series of *Neotoma* (packrat) middens at Dutch John Mountain, in the central Rockies of
 535 the western USA [93], is characteristic (see the figure). Montane conifers, including *Pinus flexilis*,
 536 *Juniperus communis*, *Pseudotsuga menziesii*, and *Juniperus scopulorum* grew at the site at LGM,
 537 and all persisted through rapid warming and increasing moisture between 15,000 and 10,000 years
 538 ago. They were joined by other trees (*Picea pungens*) and shrubs (*Krasscheninnikovia lanata*,
 539 *Gutierrezia sarothrae*, *Juniperus horizontalis*, *Holodiscus dumosa*, *Philadelphus microphyllus*, *Rhus*
 540 *trilobata*, *Cercocarpus* spp.). Many underwent local extinction during rapid warming and drying
 541 after 10,000 years ago. Most disappearances represent ‘moves’; populations of nearly all these
 542 species occur at higher elevations within 10-20 km of the site. *Juniperus osteosperma* immigrated
 543 from the south ca. 9000 years ago, and was joined by *Pinus ponderosa*; both have persisted ever
 544 since. *Pinus edulis* and *Ephedra viridis* colonized the site only 700 years ago [93][XX]. *Juniperus*
 545 *scopulorum*, *Krasscheninnikovia lanata*, and *Gutierrezia sarothrae* are long-term stayers; during
 546 their 20,000-year sojourn, they experienced a variety of environmental conditions as well as a wide
 547 variety of neighbors. *Juniperus horizontalis* occurred at the site as early as 14,000 years ago,
 548 persisting locally until ca. 6500 years ago. This species has been extirpated across the entire region;
 549 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?

575 6. When species immigrate to a site, what challenges (competition, consumption, habitat alteration)
576 and opportunities (new resources, new mutualists) do they pose for the stayers?
577
578 Paleoecological records and invasive species research are obvious places to start answering these
579 questions [2, 91, 94], but there is an opportunity to observe and model current and future dynamics
580 in a more comprehensive way.

For review only

581 BOX 3**582 People's responses to changing nature**

583

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

591

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

602

603 The redistribution of species and formation of new biotic assemblages has profound implications
604 for ecosystem functioning and human well-being [9], which depends not just on the material goods
605 and services people derive from nature but also cultural identity [97]. Sense of place and lived
606 experiences of places and landscapes help to define cultural identity and to motivate place-based

607 conservation [98]. Places are defined by their physical location, ‘materiality’ including nature, and
608 meaning to people [99]. Modern cities offer some insight into the ways people respond to ecological
609 change happening on their doorstep, and provide some evidence that people can attach to new
610 assemblages in old places [100]. The future success of place-based conservation efforts will be
611 determined in part by the willingness of people to develop new meanings for places as they change.

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612 **Figure Legends**

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

618 **Figure 2.**

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

631 **Figure 3.** Conceptual scheme showing potential response capacities of populations or species to
 632 environmental change, and potential conservation measures that might (or might not) be taken.
 633 Success of ‘stayers’ (top row) will depend on their *persistence capacity* relative to the rate and
 634 magnitude of environmental change. Persistence capacity will depend on a variety of factors,
 635 including phenotypic plasticity, evolutionary potential, genetic diversity, proximity of source
 636 populations for extinction ‘rescue’, and pressure from old and new competitors and consumers.
 637 ‘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

Figure 3

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.

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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?

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