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Managing consequences of climate-driven species redistribution requires integration of ecology, conservation and social science

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ABSTRACT

Climate change is driving a pervasive global redistribution of the planet’s species. Species redistribution poses new questions for the study of ecosystems, conservation science and human societies that require a coordinated and integrated approach. Here we review recent progress, key gaps and strategic directions in this nascent research area, emphasising emerging themes in species redistribution biology, the importance of understanding underlying drivers and the need to anticipate novel outcomes of changes in species ranges. We highlight that species redistribution has manifest implications across multiple temporal and spatial scales and from genes to ecosystems. Understanding range shifts from ecological, physiological, genetic and biogeographical perspectives is essential for informing changing paradigms in conservation science and for designing conservation strategies that incorporate changing population connectivity and advance adaptation to climate change. Species redistributions present challenges for human well-being, environmental management and sustainable development. By synthesising recent approaches, theories and tools, our review establishes an interdisciplinary foundation for the development of future research on species redistribution. Specifically, we demonstrate how ecological, conservation and social research on species redistribution can best be achieved by working across disciplinary boundaries to develop and implement solutions to climate change challenges. Future studies should therefore integrate existing and complementary scientific frameworks while incorporating social science and human-centred approaches. Finally, we emphasise that the best science will not be useful unless more scientists engage with managers, policy makers and the public to develop responsible and socially acceptable options for the global challenges arising from species redistributions.

Key words: adaptive conservation, climate change, food security, health, managed relocation, range shift, sustainable development, temperature.

CONTENTS

I. INTRODUCTION

Species across the globe, in all ecosystems, are shifting their distributions in response to recent and ongoing climate change (Parmesan & Yohe, 2003; Sorte, Williams & Carlton, 2010; Pinsky *et al.*, 2013; Alofs, Jackson & Lester, 2014; Lenoir & Svenning, 2015; Poloczanska *et al.*, 2016; Scheffers *et al.*, 2016). These shifts are faster at greater levels of warming (Chen *et al.*, 2011) and are projected to accelerate into the future with continued changes in the global climate system (Urban, 2015). Thus, there is a clear need to understand the impacts and consequences of global species redistribution for ecosystem dynamics and functioning, for conservation and for human societies (Pecl *et al.*, 2017).

Species range dynamics and climate have an intertwined history in ecological research going back centuries (Grinnell, 1917; Parmesan, 2006). However, research on species range shifts driven by contemporary climate change is relatively recent, dating back only 20 years (Southward, Hawkins & Burrows, 1995). In the past decade, research on the subject has increased dramatically (Fig. 1). While coverage is far from complete methodologically, geographically or taxonomically (Lenoir & Svenning, 2015; Brown *et al.*, 2016; Feeley, Stroud & Perez, 2016), this increased research effort highlights growing awareness that species are moving in response to climate change, worldwide (IPCC, 2014).

We believe that ‘species redistribution science’ has emerged as a field in its own right. However, to date the field has lacked strategic direction and an interdisciplinary consideration of research priorities. Historically, researchers have used ‘species range shifts’ or ‘species distribution shifts’ as favoured descriptive terms for climate-driven species movements. Here we use the term ‘species redistribution’ to encapsulate not only species movement, but also its consequences for whole ecosystems and linked social systems. Despite accumulating evidence of recent climate-driven species redistributions (Lenoir & Svenning, 2015; Poloczanska *et al.*, 2016; Scheffers *et al.*, 2016), integrated and interdisciplinary frameworks that can effectively predict the ecological, conservation and societal consequences of these changes remain uncommon [but see Williams *et al.* (2008) for a framework highlighting species vulnerability and potential management responses]. A long-term strategy for the field of species redistribution research is required to capitalise on, and respond to, the ‘global experiment’ of large-scale changes in our natural and managed ecosystems. What can be implemented now to build scientific and social capacity for adaptation to species redistribution over the next decade, the next century and beyond (IPCC, 2014)?

The ‘Species on the Move’ conference (held in Hobart, Australia, 9–12 February 2016) brought together scientists from across the physical, biological and social sciences. Here, we build on the outcomes of this conference by identifying key research directions to meet the global challenge of preparing for the impacts of climate-driven species redistribution on the biosphere and human society. We focus on directions and needs around three focal points for understanding species redistribution and its impacts: (1) species redistribution ecology, (2) conservation actions, and (3) social and economic impacts and responses. For each focal point we summarise recent trends in the field and propose priority questions for future research. We identify promising research directions and approaches for addressing these questions, placing emphasis on the potential benefits from integrating approaches across multiple disciplines and sub-disciplines. In so doing, we argue that greater interdisciplinary synthesis is fundamental to ensuring that species redistribution research continues to advance beyond simple documentation of species range shifts, to develop research programs and achieve outcomes that will inform policy and management decisions.

II. SPECIES REDISTRIBUTION AS A FIELD OF RESEARCH

To support our synthesis of future directions, we first establish how the research field of climate-driven species redistributions has evolved and quantify, bibliometrically, the prevailing research foci. To understand this history in the context of the broader scientific literature, we analysed publication trends in the peer-reviewed literature on species range shifts over the past 25 years. In total we extracted 1609 publications from Thompson Reuters *Web of Science* that contained search terms relating to distribution change or range shift (see online Supporting Information, Appendix S1 for details).

In 2006, both the proportion of range shift publications in the 'environmental sciences' and the diversity of journals publishing research on range shifts showed a clear increase (Fig. 1). At the same time, citation rates dropped relative to the discipline's baseline heralding that publications about range shifts had shifted from a few high-profile publications to mainstream ecological science (Fig. 1).

We analysed this corpus to identify research trends in two ways. First, we identified 'trending' terms. Terms were defined based on word stems, and trending terms were those that showed a significant increase in use in titles, abstracts or key words since 1995. Second, we identified 'high-impact' terms, i.e. those associated with higher than average citation rates, once we had accounted for the confounding effect of publication year. The trends analysis indicated that range shift science has become increasingly interdisciplinary over time. Terms associated with socioeconomic approaches, such as ‘ecosystem services’ have also become increasingly prevalent and tend to be associated with high-impact papers (Fig. 2). Management-oriented studies, with terms including ‘priority’ (referring to management priorities) are also increasing in use. Both socioeconomic (‘social’, ‘socioeconomic’) and management-related terms (‘complement*’ referring to complementary protection) were associated with higher than average citation rates during the period 2010–2015 (Fig. 2). Thus, we find clear evidence for the emergence of a new field that is generating increasing interest, while expanding to link with other existing and emerging fields.

III. SPECIES REDISTRIBUTION ECOLOGY

Species redistribution has been widely documented (Scheffers *et al.*, 2016) and well-developed theories have been proposed to explain how and why range shifts occur (Bates *et al.*, 2014) and how future species redistribution may proceed under global climate change (Urban *et al.*, 2016). Hence, we can consider the ecology of species redistribution under two broad and complementary areas: explanatory ecology and anticipatory ecology. Explanatory ecology generally aims to evaluate models and theory to enhance scientific understanding of the processes that drive species redistribution. For detailed reviews on subject areas specific to explanatory ecology we refer the reader to Somero (2010) (physiological factors), Blois *et al.* (2013) (biotic interactions), Maguire *et al.* (2015) (historical ecology), and Garcia *et al.* (2014) (climate trends/extreme events). Anticipatory ecology, by contrast, intends to forecast future states by inferring possible trajectories or behaviours of the system, based on parameters likely to be impacted by anthropogenic factors, such as predicting the effects of climate change on species, communities and ecosystems. For detailed reviews of anticipatory ecology we recommend Urban *et al.* (2016) and Cabral, Valente & Hartig (2016).

In this section, we do not duplicate former reviews of the explanatory and anticipatory ecology of species redistribution. Our review focuses, instead, on gaps in explanatory and anticipatory ecology (Table 1) that need to be filled in order to predict the impacts of species redistribution on biodiversity and human well-being. To achieve this aim, we examine multiple elements of explanatory ecology, including the physiological and ecological factors underpinning species redistribution, biotic interactions and historical ecology, as well as climate trends and extreme events. We conclude this section with a discussion of the challenges of anticipatory ecology.

(1) Physiological and ecological factors underpinning species redistribution

Climate change is causing pervasive impacts on ectothermic animals because of their reliance on environmental temperature to regulate body temperature (Deutsch *et al.*, 2008; Kearney & Porter, 2009). Thermal performance curves, which quantify how an ectotherm's body temperature affects its performance or fitness, are used to understand range shifts and to predict future distributions (Sunday, Bates & Dulvy, 2012; Sunday *et al.*, 2014). While thermal tolerance and performance patterns have been well studied for ectothermic taxa (Dell, Pawar & Savage, 2011), similar trends in large-scale patterns of climatic niche, e.g. heat tolerance conserved across lineages, are also apparent for endotherms and plants (Araújo *et al.*, 2013). The use of thermal performance curves in predicting species distributions often disregards ecological interactions (e.g. competition, predation, mutualism) that may be critical to population establishment and persistence (but see Urban, Tewksbury & Sheldon, 2012). In addition, the form of each species' performance curve has important effects on species interactions, with asymmetries in the thermal performance curves between interacting species likely having important impacts on the strength and outcome of interactions (Dell *et al*., 2011; Dell, Pawar & Savage, 2014). Physiological plasticity (e.g. thermal acclimation), resource specialisation, competitive interactions and behavioural thermoregulation (Thomas *et al*., 2001; Burton, Phillips & Travis, 2010; Feary *et al*., 2014; Sunday *et al*., 2014; Tunney *et al*., 2014; Tedeschi *et al*., 2016) are additional factors that can modify thermal performance curves and/or impact the nature and outcome of species range shifts.

Future research would therefore benefit from approaches that connect mechanistic processes across biological levels of organisation, from genes to ecosystems. For example, because selection acts on individual genotypes/phenotypes, an understanding of intraspecific variation in key functional traits will help in forecasting species' breadth of tolerance and capacity for range shifts (Norin, Malte & Clark, 2016). In general, both low and high variability in thermal tolerances can exist within and among populations and may vary with extrinsic factors such as environmental filtering, which causes a convergence in tolerance (i.e. heat hardening; Phillips *et al*., 2015), or intrinsic factors such as body size or life-history stages, which might result in thermal tolerance dispersion (Ray, 1960; Angilletta, Steury & Sears, 2004; Daufresne, Lengfellner & Sommer, 2009; Scheffers *et al*., 2013; Cheung *et al*., 2013).

The mechanistic basis behind variability in thermal tolerance remains poorly understood (Clark, Sandblom & Jutfelt, 2013) but may be revealed through new genetic tools (Bentley *et al.*, 2017). Measuring genetic diversity as organisms expand their range and documenting genetic structure during and after colonisation can provide a wealth of information on evolutionary dynamics of range shifts (McInerny *et al.*, 2009; Sexton, Strauss & Rice, 2011; Duputié *et al.*, 2012), but requires new, dedicated research programs and/or careful analysis of historical museum collections. Knowledge of the genetics underpinning thermal tolerance can directly inform species conservation and ecosystem restoration through assisted evolution applications (Van Oppen *et al.*, 2015).

The magnitude of range shifts can be population, species, and ecosystem dependent, suggesting determinants or mediators of species redistribution other than climate (Rapacciuolo *et al.*, 2014; Rowe *et al.*, 2015). Species redistribution studies have commonly sought to identify ecological traits that explain species responses (see Fig. 2; McGill *et al.*, 2006; Sunday *et al.*, 2015; Pacifici *et al.*, 2015). However, trait-based studies have had mixed success at identifying predictors of range shifts, with thermal niches and climate trends remaining in general the strongest explanatory variables (Buckley & Kingsolver, 2012; Pinsky *et al.*, 2013; Sommer *et al.*, 2014; Sunday *et al.*, 2015). Key traits may include those related to dispersal and establishment (Angert *et al.*, 2011; Sunday *et al.*, 2015; Estrada *et al.*, 2016), local persistence, such as intrinsic ability to tolerate changing climate (physiological specialisation; Bertrand *et al.*, 2016), phenotypic plasticity (Valladares *et al.*, 2014), micro-evolutionary processes (genetic adaptation; Duputié *et al.*, 2012), capacity to utilise microhabitat buffering effects (Scheffers *et al.*, 2013), fossorial habits (Pacifici *et al.*, 2017), and tolerance to habitat fragmentation (Hodgson *et al.*, 2012). Determining the contexts and conditions under which different traits mediate species redistribution, and to what degree those traits determine redistribution, is an important avenue of future research.

(2) Biotic interactions

In general, biotic interactions remain under-measured in range-shift studies, yet they likely play a key role in mediating many climate-induced range shifts (Davis *et al.*, 1998; HilleRisLambers *et al.*, 2013; Ockendon *et al.*, 2014). Shifts in species interactions will occur as a result of differential responses to climate by individual species that can lead to asynchronous migrations within communities and creation of novel assemblages (Pörtner & Farrell, 2008; Hobbs, Higgs, & Harris, 2009; Gilman *et al.*, 2010; Urban *et al.*, 2012; Kortsch *et al.*, 2015; Barceló *et al.*, 2016). Asynchronous shifts can also cause decoupling of trophic interactions, for example when symbiont–host interactions break down (Hoegh-Guldberg *et al.*, 2007) through mismatches in the phenology between consumers and their resources (Winder & Schindler, 2004; Durant *et al*., 2005; Post & Forchhammer, 2008; Thackeray *et al.*, 2016) or through differential thermal sensitivity of consumers and their resources (Dell *et al.*, 2014). Conversely, climate change and species distribution shifts can create novel species interactions through range expansions, as species that have evolved in isolation from one another come into contact for the first time (Vergés *et al.*, 2014; Sánchez-Guillén *et al.*, 2015).

Some of the most dramatic impacts of community change are likely to arise through the assembly of novel species combinations following asynchronous range shifts associated with climate change (Urban *et al.*, 2012; Alexander, Diez & Levine, 2015).

These predictions are supported by palaeoecological studies that show how novel species interactions resulting from past climatic changes drove profound community-level change (Blois *et al.*, 2013). The emergence of novel ecological communities will pose significant conservation and societal challenges, because most management paradigms are insufficient to cope with major reorganisation of ecosystems (Morse *et al.*, 2014; Radeloff *et al.*, 2015). Studies of the response of linked social-ecological systems to historical climatic changes are needed to inform the management of ecosystems under ongoing and future climate change (e.g. Hamilton, Brown & Rasmussen, 2003).

Contemporary observations of extreme events suggest that shifts in species interactions are particularly important when redistribution occurs in foundation (i.e. habitat-forming) or keystone species. Shifts in foundation species can initiate cascading effects on other species and act as biotic multipliers of climate change (Zarnetske, Skelly & Urban, 2012). For example, many of the greatest ecosystem impacts of climate change in marine systems have been caused by the loss of habitat-forming species such as corals, kelp forests and seagrasses (Hoegh-Guldberg & Bruno, 2010; Thomson *et al.*, 2015; Wernberg *et al.*, 2016; Vergés *et al.*, 2016).

Explanatory ecology is now shifting its focus from single species to the role of biotic interactions in mediating range shifts. A key research priority is to identify the importance of biotic interactions relative to species traits, geographic context and physical rates of change (Sunday *et al.*, 2015). A limiting factor has been the lack of multi-species ‘climate change experiments’ (Wernberg, Smale & Thomsen, 2012) and long time-series data that follow multiple trophic levels (Brown *et al.*, 2016). Thus, there is a need to join multiple data sets in order to understand how biotic interactions shape range shifts. Understanding the role of biotic interactions in species redistribution is important to inform conservation and societal challenges. For instance, models of three interacting invasive pests (potato tuber moths) in the Andes predicted that their redistribution would alter biotic interactions, which would in turn impact the level of crop damage (Crespo-Pérez *et al.*, 2015).

(3) Community redistribution and historical ecology

Despite species redistribution science being born of ecology, we are still a long way from understanding how species redistribution will drive changes in ecological communities (Marzloff *et al.*, 2016). Historical ecology suggests that climate change can result in dramatic alterations in community structure. For example, the equatorial dip in diversity evident in modern marine communities (Tittensor *et al.*, 2010) was most pronounced for reef corals during the warmer intervals of the last interglacial period (125 ka), indicating that both leading and trailing edges of species ranges were responding to increases in ocean temperature (Kiessling *et al.*, 2012). Pleistocene reef records suggest that species and communities are relatively robust to climate change and that ecological structure generally has persisted within reef coral communities over multiple climatic cycles (Pandolfi, 1996; Pandolfi & Jackson, 2006). By contrast, many North American tree species have shifted their individual distributions and adapted genetically to Quaternary climatic changes (Davis & Shaw, 2001). Human migrations, settlement patterns, and species use have also been linked to environmental change (Graham, Dayton & Erlandson, 2003). However, the rate of contemporary climate change, genetic constraints on rapid adaptation and dramatic land cover changes over the past century will challenge ‘natural’ species redistribution in the Anthropocene (Hoffmann & Sgro, 2011; Moritz & Agudo, 2013) and complicate human responses to these changes.

A key question for historical ecology is to determine the extent to which community change is driven by multiple species-specific responses to climate, *versus* shifts in key species driving cascading community change. Historical ecology can fill an important gap in our understanding, given that it focuses on systems that were, in most cases, far less influenced by humans than occur presently. Furthermore, studies in deep time allow us a glimpse into the outcome of processes similar to those that we are watching in their infancy today.

(4) Climate trends, scale mismatch and extreme events

Climate trends are a key predictor of range shifts due to the importance of climatic tolerances (or thermal performance curves) in controlling species ranges. Observational evidence of the direction of range shifts in terrestrial and aquatic environments are overwhelmingly consistent with expectations required for species to track temperature changes (Sorte *et al.*, 2010; Chen *et al.*, 2011; Comte *et al.*, 2013; Poloczanska *et al.*, 2013). Longitudinal range shifts, as well as shifts towards the tropics or lower elevations (which run counter to intuitive expectations), can be attributed to the complex mosaic of regional climate changes expected under global change that involve not only temperature but also other factors such as precipitation and land-use changes (Lenoir *et al.*, 2010; Crimmins *et al.*, 2011; McCain & Colwell, 2011; Tingley *et al.*, 2012; VanDerWal *et al.*, 2013; Pinsky *et al.*, 2013).

Multi-directional distribution shifts stem partly from the spatial arrangement of mountain ranges on land and continental shelves in the ocean, which are important physiographic features constraining (as barriers) or enhancing (as corridors) species redistribution (VanDerWal *et al.*, 2013; Burrows *et al.*, 2014). For example, the ranges of some forest plants are shifting equatorward and upward as the climate warms in France, likely due to the fact that the main mountain ranges in France are located in the south (Alps, Massif Central and Pyrenees; Kuhn *et al.*, 2016). Such geographic features may thus represent potential climatic traps or 'cul-de-sacs' for living organisms facing climate change. The northern Mediterranean Sea, for example, will likely act as a cul-de-sac for endemic fishes under future climate change (Lasram *et al.*, 2010).

A challenge in using climate variables to explain species redistribution is that species may respond to different climate variables than those available from historical measurements, due to a spatial mismatch between the size of the studied organisms and the scale at which climate data are collected and modelled (Potter, Woods & Pincebourde, 2013). For instance, relationships between climate velocity and marine species redistribution are weak or non-existent using global sea-surface temperature data sets to calculate climate velocity (Brown *et al.*, 2016), but can be strong using locally measured temperatures that coincide with organism sampling (Pinsky *et al.*, 2013). Therefore, we consider it a research priority to find ways to reconstruct high spatial- and temporal-resolution temperature histories that are relevant to the organisms under study (Franklin *et al.*, 2013; Kearney, Isaac & Porter, 2014; Levy *et al.*, 2016). This objective requires better communication and more collaboration among climatologists, remote sensing specialists and global change biologists to produce climatic grids at spatial and temporal resolutions that match organism size and thus are more meaningful for forecasting species redistribution under anthropogenic climate change.

The study of extreme events has been instrumental to species redistribution research, because punctuating events provide distinct natural experiments for the study of biological responses to climate change. The frequency and amplitude of extreme events is increasing with climate change (IPCC, 2013), placing increasing emphasis on studying extreme events in the context of longer-term change. Impacts of climate change on biological communities are often mediated by extreme events (Fraser *et al.*, 2014; Thomson *et al.*, 2015; Wernberg *et al.*, 2016). For example, ocean temperatures along the western Australian coast increased for over 40 years, with kelp forests exhibiting little noticeable ecological change, but a marine heat wave drove a 100 km kelp forest range contraction in only two years (Wernberg *et al.*, 2016). The infrequent nature of extreme events means that long time series are required to document the cumulative impacts on ecosystems. For example, in Australia, severe wildfires in quick succession brought about an ecosystem regime shift in mountain ash forests (Bowman *et al.*, 2014). A research priority is therefore to extend studies that document changes arising from a short-term extreme event into longer time series that may allow us to understand the cumulative effects of changes in frequency of extreme events.

(5) Anticipating future redistributions

The urgency of responding to anthropogenic climate change has stimulated a shift towards anticipatory ecology that aims to predict future ecological change. The shift to anticipatory ecology is indicated by our literature analysis, which found an increased frequency of terms related to prediction [Fig. 2; terms ‘sdm’ (species distribution model) and ‘maxent’ (a popular tool for such modeling); Phillips & Dudík (2008)]. Approaches to predicting the consequences of climate change for biodiversity are varied and include correlative species distribution models (SDMs; Guisan & Zimmermann, 2000) as well as mechanistic and hybrid SDMs that account for physiological constraints, demographic processes or environmental forecasts (Kearney & Porter, 2009; Hartog *et al.*, 2011; Webber *et al.*, 2011; Dullinger *et al.*, 2012; Cheung *et al.*, 2015; Table 1). The emergence of the study of species redistributions during the era of rapidly increasing computing power and growing availability of climate data has also contributed to the dominance of spatial modelling techniques. The emphasis on forecasting has been paralleled by a development of predictive techniques, including machine-learning algorithms such as maxent (Phillips & Dudík, 2008).

Anticipatory models have recently been progressing on two fronts. First, mechanistic and process-based models, often including physiology, biotic interactions, and/or extreme events, are increasingly being used and developed for biogeographic prediction (Kearney & Porter 2009; Cabral *et al.*, 2016). Bioenergetics models, for example, can overcome traditional species distribution model limitations when making predictions under novel climates, modelling extreme events and understanding the importance of timing of weather events (e.g. Briscoe *et al.*, 2016). Mechanistic models tend to be data intensive and have so far been little used in conservation planning despite significant potential (Evans, Diamond & Kelly, 2015; Mitchell *et al.*, 2016). However, prospects for process-based models integrating conservation and society are positive, as models become more flexible, accurate, and accessible (Kearney & Porter, 2009).

The second trend with predictive models has been an increasing focus on physical drivers at appropriate spatial and temporal scales (Potter *et al*., 2013). In this regard, a key perspective in species redistribution is the velocity of climate change – which measures the geographic movement of temperature isotherms (Loarie *et al.*, 2009; Burrows *et al.*, 2011) to project changes in species ranges and community composition (Hamann *et al.*, 2015). Climate velocity trajectories (Burrows *et al.*, 2014) based on sea surface temperatures, for example, were recently combined with information on thermal tolerances and habitat preferences of more than 12,000 marine species to project that range expansions will outnumber range contractions up to the year 2100. Broadened ranges, in turn, are projected to yield a net local increase in global species richness, with widespread invasions resulting in both homogenised and novel communities (Molinos *et al.*, 2015). However, velocity measures have limitations and can underestimate climate change exposure for some communities (Dobrowski & Parks, 2016). For marine systems, changes in the speed and direction of currents can potentially influence dispersal and therefore population connectivity, and may also need to be considered for a more complete understanding of the relationship between climate drivers and rates and magnitudes of range shifts (Sorte, 2013; Cetina-Heredia *et al.*, 2015). High-resolution particle-transport Lagrangian models may be useful in this context (van Gennip *et al.*, 2017). Ultimately, examining multiple climate change metrics and linking them to the threats and opportunities they represent for species could overcome the limitations of individual metrics and provide more-robust impact estimates (Garcia *et al.*, 2014).

IV. CONSERVATION ACTIONS

Faced with climate change as a novel and substantial threat, a new species-management paradigm has emerged (Stein *et al.*, 2013): to be effective, conservation strategies must account for both present and future needs and must be robust to future climate change. Such strategies will require integration of species redistribution science with consideration of the social and economic consequences (Table 1). Managers have several options for conserving species and ecosystems faced with range shifts: adapt conservation management in current landscapes and seascapes; facilitate natural species movement; manage resources to support species redistribution; and/or move species as a conservation intervention, i.e. managed relocation. Important reviews on conservation under climate change, such as Heller & Zavaleta (2009) and Mawdsley, O'Malley & Ojima, (2009), provide context for adaptation strategies under warming. In this section we specifically aim to synthesise recent advances in species redistribution science and conservation actions that attempt to accommodate species redistributions, requiring the involvement of multiple stakeholders for effective implementation.

(1) Adapting management in current conservation landscapes and seascapes

Mitigating the impacts of climate change on species and ecosystems *in situ* is challenging, because it requires management decisions that are robust to future change and the development of adaptive solutions for specific populations (e.g. providing shelter or supplemental food; Correia *et al.*, 2015). Systematic conservation planning efforts are increasingly incorporating the principles of climate change adaption into the protected-area design process (Carvalho *et al.*, 2011; Groves *et al.*, 2012), ensuring that existing protected areas are resilient to climate change by maintaining and increasing the area of high-quality habitats, prioritising areas that have high environmental heterogeneity, and controlling other anthropogenic threats (Hodgson *et al.*, 2009). Habitat engineering may also be required to provide effective recovery and maintenance of populations, for example, through the installation of microclimate and microhabitat refuges or enhancement and restoration of breeding sites (Shoo *et al.*, 2011). Identification of microrefugia, small areas robust to warming impacts over long time periods, will also be key for long-term planning (Lenoir, Hattab & Pierre, 2017). In many countries, the legal and governance framework underpinning protected-area management may not yet allow for these types of active management interventions (McDonald *et al.*, 2016*a*), so legal reform may be needed.

(2) Facilitating natural species movement

As the most suitable habitat conditions for species are shifting geographically under climate change and species redistribute themselves, forward planning is increasingly essential, both temporally and spatially (Mawdsley *et al*., 2009). Although most palaeoecological studies (e.g. Williams & Jackson, 2007) indicate that range shifts alone do not drive widespread extinction events [but see Nogués-Bravo *et al.* (2010) who did find evidence for extinctions], range-restricted species potentially face high climate-driven extinction risks (Finnegan *et al*., 2015; Urban, 2015).

Reserve networks must consider current biodiversity, probable patterns of future biodiversity, corridors suitable for projected range shifts, and cost (Scriven *et al.*, 2015; Lawler *et al.*, 2015), anticipating the need for protected-area establishment in newly suitable areas (Carvalho *et al.*, 2011). Climate-velocity methods (Burrows *et al.*, 2014) or the analysis of fine-scaled climatic grids (Ashcroft *et al.*, 2012) can be used to identify climate refugia – places where microclimates are decoupled from macroclimatic fluctuations and are thus more stable and less likely to change quickly – as potentially good candidates for future protected areas. Information on future habitat suitability for threatened species (e.g. obtained using SDMs) can be coupled with information on climate refugia to target areas likely to maximise conservation benefits (see Hannah *et al.*, 2014; Slavich *et al.*, 2014). To assess landscape or seascape connectivity with greater realism, patterns of habitat fragmentation (McGuire *et al.*, 2016) and flow must be considered, i.e. wind and oceanic currents (van Gennip *et al.*, 2017; Péron *et al.*, 2010; Sorte, 2013).

In some cases, facilitating species redistribution can be achieved through the expansion or realignment of existing protected area boundaries. Where public conservation funding is limited, it may be necessary in some circumstances to release protection of some areas in order to secure others of higher priority (Alagador, Cerdiera & Araújo, 2014). In addition to maintaining connectivity through reserve network design, market-based instruments and public–private partnerships can be harnessed to accommodate species redistribution. Conservation easements, for example, while popular and potentially effective in environmental protection of private land, rarely consider climate change impacts or species redistribution (Rissman *et al.*, 2015). New mechanisms for private land stewardship and management, including Indigenous Protected Area (IPA) agreements, will also be needed.

Conservation interventions designed to meet contemporary environmental challenges can conflict with climate change planning objectives. For example, fences in Africa around wildlife reserves have been good for minimising human–wildlife conflict but poor for maintaining landscape connectivity (Durant *et al.*, 2015). Similarly, shifts in agriculturally suitable areas in the Albertine region of Africa, as a result of changing climate, may cause a displacement of agriculture into protected areas, significantly complicating climate-driven species redistribution impacts on conservation plans for the region (Watson & Segan, 2013).

(3) Resource-management systems for species redistribution

Some existing resource-management systems can be extended for adaptive management of species on the move. For example, a real-time management system is used in eastern Australia to predict the distribution of a tuna species over the cycle of a fishing season (Hobday & Hartmann, 2006; Hobday *et al.*, 2011). The changing distribution of the fish requires dynamic responses to zones that restrict fishing activity. While this example of species redistribution is on a seasonal timescale, the management system can also respond to long-term species redistribution, based on regular updates of the management zones. Such real-time management responses to changing species distributions are relatively advanced in marine systems and are being formalised in the field of dynamic ocean management (Hobday *et al.*, 2014; Lewison *et al.*, 2015; Maxwell *et al.*, 2015).

Conservation strategies for mobile and range-shifting species can also utilise innovative market-based instruments and develop new partnerships involving private landholders. A promising example is The Nature Conservancy’s California pop-up wetland initiative, which involves seasonal land ‘rentals’, in which farmers agree to flood their fields to facilitate water bird migration (McColl *et al.*, 2016). Predictive habitat modelling of bird migration is used to earmark different land parcels, and landholders submit bids to participate in each year’s habitat creation program. As in this example, local and regional conservation planning for multiple uses requires good-quality data, plus resources for monitoring and implementation. Researchers also need to understand what information land-owners, planners and policy makers actually need to aid decision-making, which requires considerable engagement and knowledge exchange (Cvitanovic *et al.*, 2015).

As part of this engagement, structured decision-making processes can inject both values and scientific data into the development of management strategies for ecosystem-based marine management, as proposed for development of high seas protected areas (Maxwell, Ban & Morgan, 2014). Options for managers and policy makers can be evaluated with quantitative modelling tools, such as models of intermediate complexity (Plagányi *et al.*, 2014), while management strategy evaluation (Bunnefeld, Hoshino & Milner-Gulland, 2016) can be used to test climate-smart management strategies that include socio-ecological criteria. In addition to novel dynamic management approaches, existing tools in development and conservation law, such as biodiversity offsets, will need to be modified to promote adaptive conservation planning for species redistribution (McDonald, McCormack & Foerster, 2016*b*) and to allow management responses on appropriate timescales (Hobday *et al.*, 2014).

(4) Managed relocation

Given numerous decision frameworks for managed relocation, the science required to inform any decision to relocate a species is defined by knowledge gaps in local species ecology and management (e.g. Richardson *et al.*, 2009; McDonald-Madden *et al.*, 2011; Rout *et al.*, 2013 and see Article 9 in Glowka *et al.*, 1994). Trial introductions of the critically endangered western swamp turtle (*Pseudemydura umbrina*) to the south-western corner of Australia (300 km south of its native range), in 2016, serve as a useful example. For the turtle, persistence in the wild is constrained by severe habitat loss and fragmentation and by a rapid reduction in winter rainfall. Correlative SDMs based on coarse-grained climatic data have created a challenge for translocation planning, as the turtle historically occupies just two wetlands 5 km apart (Mitchell *et al.*, 2013). The solution has been to build mechanistic SDMs that are based on detailed knowledge of the turtle's physiological limits, behaviour, and the ecohydrology of their ephemeral wetland habitats (Mitchell *et al.*, 2013, 2016). Forcing these process-based SDMs with future drier and warmer climates has illustrated where suitable habitat might exist into the future, and when complemented with spatially explicit multiple criteria analysis (Dade, Pauli & Mitchell, 2014) has identified candidate wetlands for future attempts to establish outside-of-range populations.

The primary challenge for practicing managed relocation is identifying ways to overcome any social barriers to relocation. Relocating species for conservation can challenge deeply held values and beliefs about human intervention in nature, and what constitutes appropriate and desirable environmental stewardship. Particular challenges may arise for Indigenous peoples, for whom connection to landscapes and historically, culturally and spiritually significant species is of great importance. Formal mechanisms for engaging with local communities and stakeholders, including consideration of the cultural effects and drivers of proactive conservation management under climate change, will be critical. Issues include cultural nuances, such as the terminology used in management proposals and policy. For example the term ‘assisted colonisation’, adopted in the guidelines of the International Union for Conservation of Nature (IUCN) for species introductions outside of the known range to prevent extinction, has historical and colonial connotations with the word ‘colonisation’ that may create barriers to participation. In this case, an alternative, culturally considerate phrase to encourage broader inclusion might be ‘managed relocation’ (see Schwartz *et al.*, 2012).

The IUCN guidelines for conservation translocations (IUCN/SSC, 2013) provide a complete framework to assess the need for managed relocation, including the risks associated with translocations for the species of interest and for the ecosystem that receives the new species. Potential damage to the ecosystem from managed relocation is the worst-case scenario, and this issue forces decision-makers to ask themselves what they value most. Is the survival of a particular species that is threatened by human actions sometimes worth the risk of profound change to the recipient ecosystem? If we aim for a species to thrive, when does it become invasive? These are questions that will need to be answered as managed relocation for conservation becomes more frequent. Legislative reform is also required to change the regional and domestic laws and policies that guide practical implementation of managed relocations. Many jurisdictions around the world have no explicit legal mechanisms for relocating species across jurisdictional borders, a regulatory gap that is likely to become more problematic under rapid climate change

(Schwartz *et al.*, 2012). Law and policy should incorporate collaborative mechanisms for cross-tenure, local, regional and international species relocations, and should facilitate species relocation to support broader ecological processes, not just to preserve charismatic threatened species.

V. SOCIAL AND ECONOMIC IMPACTS OF SPECIES REDISTRIBUTION

Changing distributions of economically and socially important species under climate change are affecting a wide range of peoples and communities. Understanding the ecology of species on the move and the development of conservation tools for species redistribution responses will, together, contribute to an integrated approach to managing social impacts (Table 1). Consequences will likely include exacerbated food security issues; challenges for Indigenous and local livelihoods, governance and cultures; and human health problems. Facing these challenges will require an interdisciplinary, participatory approach (O'Brien, Marzano & White, 2013) that will include not only scientists and professionals from different fields but also managers, governments and communities.

(1) Food security

Since the spike in food prices in 2008, much thought has gone into how to feed nine billion people by 2050 (World Bank, 2008; Evans, 2009; Royal Society of London, 2009). A key to producing 70–100% more food by 2050 will be filling the yield gap for agriculture (Godfray *et al.*, 2010), i.e. the difference between potential and actual yields. For fisheries and aquaculture, the challenge is to provide an additional 75 Mt of fish by

2050 to supply 20% of the dietary protein needed by the human population (Rice & Garcia, 2011). Given that yields from capture fisheries have already plateaued, most of the additional fish will need to come from aquaculture (FAO, 2014).

The challenges of enhancing agricultural and fisheries productivity to meet global food demand (Godfray *et al.*, 2010; FAO, 2014) are exacerbated by species redistribution. Increased agricultural productivity will depend in part on keeping weeds, diseases and pests in check where they increase in abundance and disperse to new areas. As fish species migrate in search of optimal thermal conditions, the locations of productive fisheries will change (Cheung *et al.*, 2010), resulting in gains for some communities and losses for others (Bell *et al.*, 2013). Changes in the distributions and relative abundances of harmful marine algae, pathogens and pests, will also create new hurdles for fisheries and aquaculture (Bell *et al.*, 2016).

A key short-term priority for food-security research is the development of new global models of fishery production that account for climate change. Several models are now being used to inform large-scale policy on global change in marine fishery production (e.g. Cheung *et al.*, 2010, Barange *et al*., 2014). However, a single approach (Cheung *et al.*, 2010) has been dominant in representing species redistributions. While this model has been repeatedly updated (Cheung *et al.*, 2016, Cheung & Reygondeau 2016), considerable structural uncertainty remains in our ability to predict change in fishery production, as production depends critically on uncertain future fishery-management arrangements (Brander, 2015). The extent to which structural uncertainty afflicts global production estimates needs to be evaluated with alternative modelling approaches. These issues are beginning to be addressed by model ensemble initiatives such as through the

Inter-sectoral Model Intercomparison Project (https://www.isimip.org/) and through the inclusion of more detailed bio-economic processes (Galbraith *et al*., 2017).

(2) Indigenous livelihoods, governance and cultures

The distributions and relative abundances of species within their historic ranges have been central to the knowledge of Indigenous peoples, including not only sedentary communities, but also mobile communities such as nomads, pastoralists, shifting agriculturalists and hunter-gatherers (Kawagley, 2006; Sheridan & Longboat, 2006; Arctic Council, 2013; Mustonen & Lehtinen, 2013). Maintaining relatively intact ecosystems is crucial to the preservation of livelihoods, cosmologies, cultures and languages of these groups, and many have developed governance systems for their biological resources based on holistic observations and checks-and-balances to prevent overharvesting (Huntington, 2011; Mustonen, 2015; Mustonen & Mustonen, 2016). Alterations in species ranges and relative abundances due to climate change will have profound consequences for these governance systems.

Leaders of these societies also recognise that changes in relative abundances of species are caused by other drivers, such as extraction of natural resources and development of infrastructure (Arctic Council, 2013), and have called for a paradigm shift in governance to address the profound changes underway (Kawagley, 2006; Huntington, 2011). This paradigm shift requires partnership approaches with non-Indigenous institutions to respond to the scale and significance of impacts on livelihoods (Huntington, 2011). Culturally safe and respectful language spoken by scientists, and teaching of science for Indigenous, traditional and mobile peoples are an essential part of this approach. Otherwise, opportunities to effectively integrate the often deep and diverse knowledge of these people into strategies to cope with change will be lost (Lee *et al.*, 2016).

(3) Human health

The risk of increases in infectious diseases due to species redistributions, potentially exacerbated by food insecurity crises, is also a significant concern (Altizer *et al.*, 2013) and a key research challenge. History is full of examples of climate-driven species movements and human distribution shifts, resulting in infectious disease outbreaks (McMichael, 2012). For example, bubonic plague outbreaks caused by the bacterium *Yersinia pestis* during the Black Death – the great pandemic originating in Asia and spreading throughout Europe between 1347 and 1353 – have been shown to occur roughly 15 years after a warmer and wetter period (Schmid *et al.*, 2015). Even the contemporary dynamics of bubonic plague, which still occurs in Central Asia, have been clearly linked to climate change (Stenseth *et al.*, 2006).

In the Arctic, many interconnected factors such as climate, wildlife populations, and health have triggered infectious disease outbreaks. Although the health of Indigenous peoples of the circumpolar region has improved over the last 50 years, certain zoonotic and parasitic infections remain higher in Arctic Indigenous populations compared to respective national population rates (Parkinson & Evengård, 2009). Evidence for associations between climate and infectious disease in the Arctic is clear, but the relationship between climate change and vector-borne disease rates is poorly explored, owing to the small number of studies on the subject (Hedlund, Blomstedt & Schumann, 2014). However, the case of increasing incidence of tick-borne encephalitis in Sweden since the 1980s is instructive: mild winters have increased tick population densities in the country, leading to increased disease incidence (Lindgren & Gustafson, 2001). A key component of prevention and control of climate-mediated infectious diseases is surveillance.

(4) Need for monitoring

More modelling is needed to understand the cascading effects of climatic changes on the species that we rely on for food and livelihoods and those whose spread can adversely affect human health. Such modelling will help identify practical adaptations and the policies needed to support them.

Collection of the information needed to validate these models can be enhanced by community-based monitoring and citizen science, engaging the agriculture, fishing and aquaculture industries and Indigenous and local communities (Mayer, 2010; Johnson *et al.*, 2015; Robinson *et al.*, 2015). These groups are well placed to monitor changes in the relative abundance and distribution of species that they rely on or regularly interact with. For many Indigenous and local communities, monitoring is central to the preservation of their sea- and land-use patterns and sustainable development (Sheridan & Longboat, 2006; Mustonen, 2015). Moreover, rapidly developing tools and networks in citizen science may enhance large-scale monitoring (Chandler *et al.*, 2016). For example, citizen science has already contributed approximately half of what we know about migratory birds and climate change (Cooper, Shirk & Zuckerberg, 2014). Broad stakeholder engagement has the added benefit of increasing awareness of the effects of climate change on human well-being, while empowering communities to effect changes in environmental behaviour and policies.

Involving local stakeholders in monitoring also enhances management responses at the local spatial scale, and increases the speed of decision-making to tackle environmental challenges at operational levels of resource management (Danielsen *et al.*, 2010). The promptness of decision-making in community-based monitoring and the focus of the decisions at the operational level of species and resource management make community-based monitoring approaches particularly suitable when species are rapidly shifting ranges. Community-based monitoring is also likely to provide information about crucial new interactions between species (Alexander *et al.*, 2011; Huntington, 2011). One potential challenge to community-based monitoring is that, in situations in which constraints or demands on resources may condition quotas or financial payments to communities, the local stakeholders might have an incentive to report false positive trends in those natural resources so they can continue to harvest the resources or continue to be paid, even though the resources may actually be declining (Danielsen *et al.*, 2014). Systems ensuring triangulation and periodic review of the community-based monitoring results will therefore be required, whether the monitoring is implemented by communities, governments or the private sector.

Increased monitoring may also increase understanding of the spatial and temporal impacts on human societies posed by changes in the distribution and abundance of species. The effects of climate change on species needs to be mainstreamed into routine food-production assessments so that society is prepared and can adapt to predicted changes. Technological improvements have increased the potential for citizen scientists to engage in the necessary monitoring (Brammer *et al.*, 2016) and for industries to capture essential data as part of routine field operations (Ewing & Frusher, 2015). On a broader scale, co-ordination of monitoring to obtain data that can be compared across diverse regions is needed. Identification of hotspots, where range changes and impacts are expected to be seen earlier (Hobday & Pecl, 2014; Pecl *et al.*, 2014), can aid in the early development of broad-based practical adaptive strategies. Moreover, technological advances are making it possible to not just monitor the location of organisms, but understand the physiological and behavioural processes underlying their movement patterns (Block *et al.*, 2001; Clark *et al.*, 2008, 2010). An integrated understanding of the drivers of species movement will greatly strengthen our capacity to plan for species redistributions in the future.

VI. INTERDISCIPLINARY APPROACHES TO ADDRESS SPECIES REDISTRIBUTION CHALLENGES

Species redistribution is a complex phenomenon dependent upon multiple and interacting multiscale climatic variation, as well as social and ecological/evolutionary processes (Fig. 3). The formation of novel species assemblages as a consequence of this redistribution brings significant new challenges for governments, resource users and communities, particularly when dependence on natural resources is high or where present or future species ranges cross jurisdictional boundaries (Pecl *et al.*, 2011). Identifying the mechanisms and processes driving species redistributions is critically important for improving our capacity to predict future biological change, managing proactively for changes in resource-based human livelihoods and addressing conservation objectives (Pinsky & Fogarty, 2012).

In recent years, the scientific study of climate-driven species redistribution has matured significantly (Fig. 1). Although research continues to focus on modelling and prediction of distribution shifts, researchers have increasingly incorporated management and socio-economic considerations explicitly (Fig. 2). As this review has highlighted, biological studies and management and social science research on species redistribution have provided a wealth of insights into global change, and have supported several innovative management responses (i.e. managed relocation, real-time management systems). Nevertheless, many challenges and key questions require answers (Table 1). Further integrated development will require working across disciplines to find innovative solutions (Bjurström & Polk, 2011).

Long-term interdisciplinary research programs that integrate the natural and social sciences are needed to study, understand and model the impact of climate-driven species redistribution on ecosystem functioning. More specifically, interdisciplinary research is needed on changes to multiple ecosystem services (e.g. food) and disservices (e.g. diseases) delivered to society, as climate changes, particularly as interdisciplinary approaches are not well represented in climate research (Bjurström & Polk, 2011). Simultaneous socio-ecological time series often reveal that people respond to ecosystem change in surprising ways. For example, a climate regime shift around 1960–1990 drove declines of a cod fishery, but opened up opportunities for a new shrimp fishery off Greenland (Hamilton *et al*., 2003). However, only communities with sufficient capital to invest in new fishing gear, and entrepreneurial individuals who were willing to invest in a new fishery were able to adapt to the ecosystem change. Thus, societal responses to species redistributions can be highly dependent on a few individuals, and human responses and natural changes must be considered in combination (Pinsky & Fogarty, 2012).

Many challenges must be overcome to execute a successful long-term interdisciplinary research program. Even within fields such as ecology, disciplinary barriers threaten to limit advances in species redistribution research. For example, communication and collaboration between marine and terrestrial researchers (Webb, 2012) has the potential to spark key developments. Unfortunately, research proposals with the highest degree of interdisciplinarity currently have the lowest probability of being funded (Bromham, Dinnage & Hua, 2016). Although long-term monitoring programs provide the essential foundation for tracking and understanding the causes and consequences of species redistributions, they also encounter funding difficulties due to the long time span of funding required and a bias in grant agencies away from studies perceived as simply observational research and towards hypothesis-driven research (Lovett *et al.*, 2007). Institutional change in funding agencies and an emphasis on prioritising interdisciplinary and long-term projects could lead to important, high-impact climate change research (Green *et al.*, 2017). In the meantime, global change scientists also need to explore multiple options to support long-term and interdisciplinary studies, such as harnessing citizen science and engaging in large-scale collaborative efforts.

In fact, citizen science may help to fill the knowledge gap in long-term and spatially extensive studies (Breed, Stichter & Crone, 2013). Citizen science approaches typically involve recruiting observers to be part of a formal program, a method for recording meaningful data, and a means of making those data accessible and discoverable for later use. In addition, successful programs often include data-vetting and data-management practices to ensure the integrity and long-term availability of data, providing data products to contributors and other interested parties, and interpreting the results of these efforts to tell a story of environmental functioning or change to larger audiences. Further work is needed, however, to find suitable ways to connect citizen science and community-based monitoring programs with international biodiversity data repositories (Chandler *et al.*, 2016).

Growing recognition of the important role of Indigenous, traditional and mobile peoples in protected area management is one positive change in recent years. The creation of a fourth type of governance (in addition to government, shared and private governance) in the IUCN's Protected Area Guidelines specifically addresses IPAs and Indigenous peoples' and Community-Conserved territories and Areas (ICCAs). In this case, the nature–culture binary is being dismantled to incorporate a range of worldviews that promote sustainable development, governance vitality and management devolution (delegation of power) (Borrini-Feyerabend *et al.*, 2013; Lee, 2016). Acknowledging the legitimacy of traditional knowledge systems can be instrumental in understanding species redistribution and provides a mechanism by which local communities can monitor and manage impacts (Eicken *et al.*, 2014; Tengö *et al.*, 2017).

Examples of on-ground management responses to shifting species are few, to date, and those that have been reported are based on seasonal or short-term responses to changes in species distribution (Hobday *et al.*, 2011, 2014; McColl *et al.*, 2016). These few examples do illustrate how long-term change might be accommodated, but such approaches may not support management responses for the transformational level of change that may be needed in some regions. In these cases, development of long-term adaptive pathways (sensu Wise *et al.*, 2014) for species on the move is required. These pathways can include decision points at which switching of strategies is required, for example defining at what point a habitat-creation strategy should be changed to a translocation strategy.

VII. CONCLUSIONS

(1) Until recently, species redistribution was seen as something that would happen in the future rather than an immediate issue. However, it is happening now, with serious ecological and societal implications and impacts already being observed.

(2) The cross-cutting nature of species redistribution calls for the integration of multiple scientific disciplines, from climate science to ecology, palaeoecology, physiology, macroecology, and more. We further suggest that research on contemporary species redistribution needs to span process-based studies, observational networks by both scientists and community members, historical data synthesis and modelling over a variety of scales.

(3) Species redistribution defies conservation paradigms that focus on restoring systems to a baseline and challenges environmental management strategies, which are often static and based on human-dictated boundaries drawn in the past. Climate-driven species redistribution therefore presents both fundamental philosophical questions and urgent issues relevant to conservation and society.

(4) For species redistribution research to support development of relevant adaptive strategies and policy decisions adequately, studies need to take an interdisciplinary approach and must recognise and value stakeholders. Involving stakeholders in monitoring and collection of data offers an opportunity to help guide effective adaptation actions across sectors.

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X. SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Appendix S1. Details of extraction and analysis of research foci in the field of species redistribution.

Table S1. List of 109 ‘trending’ terms defined as word stems that significantly increased in annual frequency of appearance in publications on species redistribution since 1995.

Table S2. List of 49 ‘high-impact’ terms defined as word stems associated with higher than average citation rates, accounting for publication year.

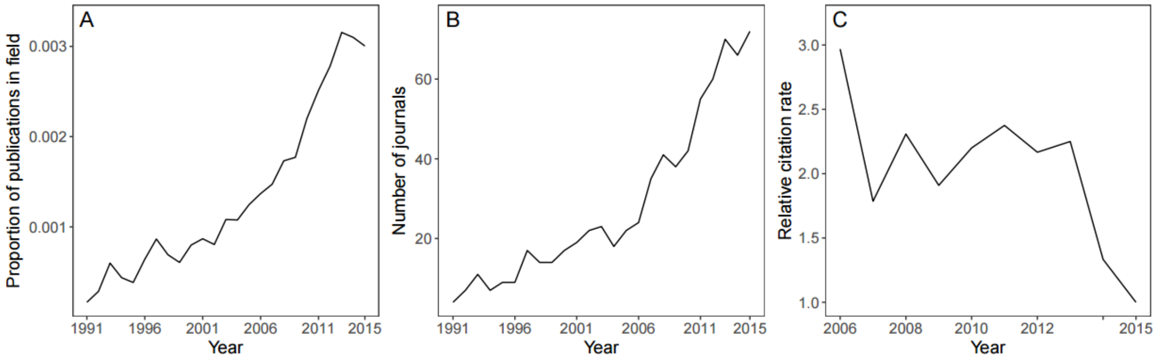

Fig. 1. Publication trends for papers on species range shifts. (A) Proportion of publications addressing species redistribution over a time, as a fraction of all papers in environmental sciences/ecology fields. (B) Number of journals publishing species redistribution papers over time. (C) Median annual citation rate of species redistribution papers decreases to the median annual citation rate of papers in the general environmental sciences/ecology field.

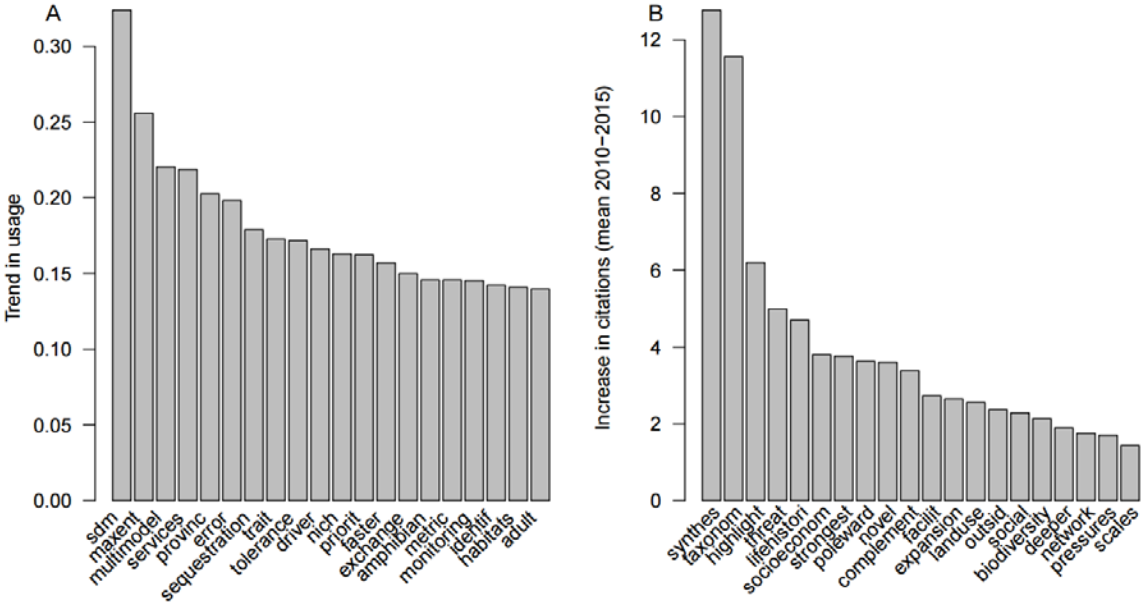

Fig. 2. Analysis of trends used within the species redistribution literature: (A) top 20 trending words that increased significantly in usage, and (B) top 20 high-impact words that correspond with increased citation rates of papers published between 2010 and 2015. See Supporting Information for details of the analysis. sdm, species redistribution model.

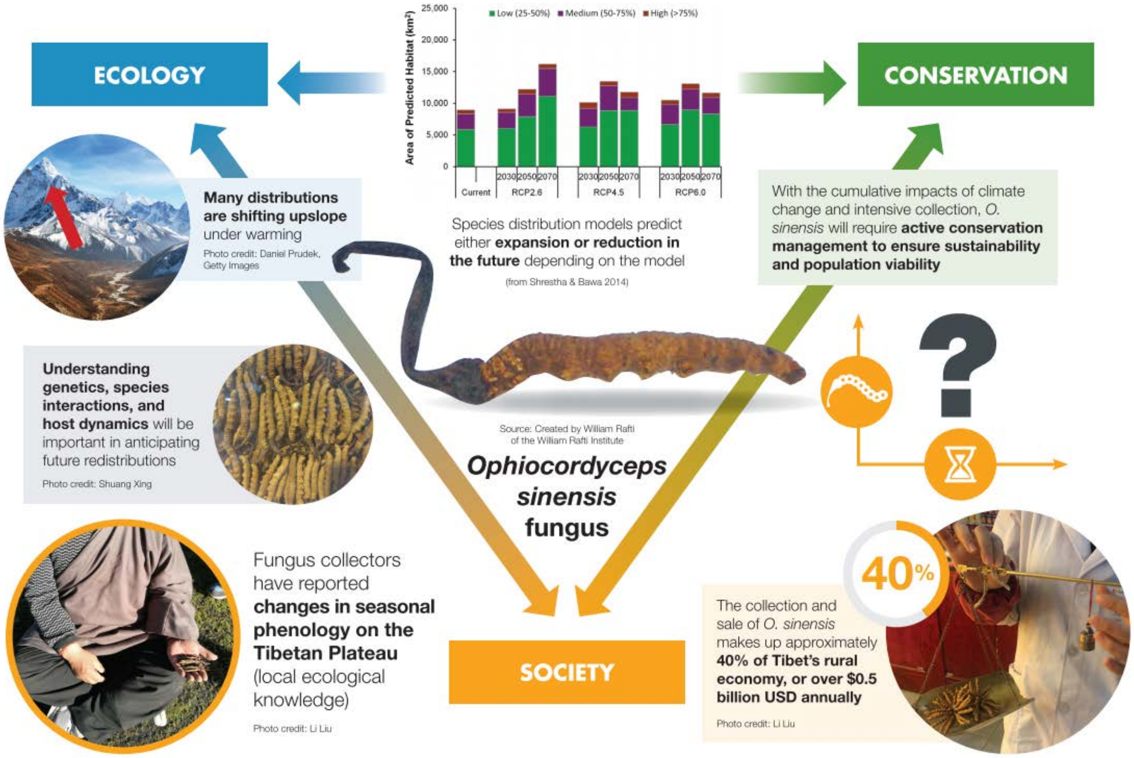

Fig. 3. *Ophiocordyceps sinensis*, a caterpillar-feeding fungus of the Tibetan plateau, presents a useful case study for the importance of an integrated and interdisciplinary approach to species redistribution. The species is widely consumed throughout China, largely for medicinal purposes. Distribution shifts of the species in recent decades have been observed, but models under future climates have yielded divergent outcomes (both range expansion and reduction) based on different sets of data and approaches (Yan *et al.*, 2017). Open questions remain about the physiology of the species and, particularly critical in this case, how interactions with the host caterpillar species might change under warming. *O. sinensis* is a critical part of the Tibetan economy (Winkler, 2008) but is also vulnerable to extinction given intensive collecting pressure and possible climate change impacts (Yan *et al.*, 2017). Greater understanding of the ecology of the species will assist

in addressing economic and conservation challenges. But, equally importantly, the Indigenous populations that depend upon *O. sinensis* for income can also provide invaluable insights into complex ecological systems and how climate change might be changing these systems (Klein *et al.*, 2014).

Table 1. Key questions posed by attendees of the 2016 *Species on the Move* conference and additional questions developed for each research focus: Ecology, Conservation and Society. Also included for each key question are cross-cutting themes (*sensu* Kennicutt *et al.*, 2015). ECO, Ecology; CONS, Conservation; SOC, Society; SDM, species redistribution model.

Key questions and topics	**Approaches and interdisciplinary cross-cutting**	**References**
Ecology		
To what extent will novel species combinations impact future change to ecological communities? **CONS**/**SOC**	Experimental manipulation Modelling	Urban *et al.* (2012) Alexander *et al.* (2015)
How much do biotic interactions affect range shifts, compared to the effects on ranges from species traits, geographic context and physical rates of change? **CONS**	Incorporation of species interactions into SDMs Palaeoecological methods	Ferrier *et al.* (2007) Wisz *et al.* (2013) Blois *et al.* (2013) Fitzpatrick *et al.* (2013)
How can we predict species responses to extreme events? Much empirical physical research is focused on extreme events, but most biological/ecological modelling evaluates slow long-term change. **CONS**/**SOC**	Incorporate extreme climatic events into modelling/predictions Measure key mechanistic processes	Zimmermann *et al.* (2009) Azzurro *et al.* (2014) Briscoe *et al.* (2016)
What is the role of plasticity (physiological, behavioural) in mediating species responses within and between populations, and how does plasticity affect modelling predictions? **CONS**	Accounting for intraspecific differences in realised niche	Valladares *et al.* (2014) Bennett *et al.* (2015)

What are the main determinants of time lags in biotic responses to climate change (the climatic debt)? **CONS**	Explaining magnitude of lags in response to climate change in addition to the magnitude of the shift	Bertrand *et al.* (2016)
How will uncertainty in climate change projections affect predictions of species redistribution? **CONS**	Multi-model ensemble averaging	Fordham *et al.* (2011)
How can co-occurring taxa/communities best be modelled under changing climates? **CONS**	Community-level models	Maguire *et al.* (2016)
Conservation		
How can we integrate uncertainty into the conservation planning process? What time frame allows for robust actions while minimising uncertainty? **SOC**	Decision science	Shoo *et al.* (2013)
How can we monitor large-scale landscapes and seascapes and complex natural and social interactions best across regions? **ECO**/**SOC**	Monitoring to adjust (adaptive) conservation actions continuously Interpretation of satellite remote-sensing, population surveys	Tøttrup *et al.* (2008) Pettorelli *et al.* (2014) Kays *et al.* (2015)
What are the values and risks associated with novel communities that arise from individual species range shifts? What are the effects of invasive species on the maintenance of phylogenetic and functional diversity? **ECO**	Assessing functional and phylogenetic diversity Palaeoecological methods	Buisson *et al.* (2013) Albouy *et al.* (2015)

How do we apply prescriptive/assisted evolution to accommodate species redistribution? **ECO**	Molecular ecology Conservation genomics	Smith *et al.* (2014) Hoffmann *et al.* (2015)
How can we build dynamic conservation management strategies that cope with changes in species distributions? **SOC**	Sequential dynamic optimsation	Alagador *et al.* (2014)
How does climate change interact with other drivers of biodiversity change (e.g. invasive species, land use and fire) to influence outcomes for biodiversity (all species)? **ECO**/**SOC**	Management of local stressors Coupled population and SDMs	Russell *et al.* (2009) Bonebrake *et al.* (2014) Jetz et al. (2007)
Will microrefugia allow species to persist locally as climate changes? If so, where are they? **ECO**	Climate change metrics Fine-scale grids	Keppel *et al.* (2012) Ashcroft *et al.* (2012)
Society		
How do species redistributions impact ecosystem services through biodiversity reshuffling? **ECO**	Coupled SDM and trait-based methods	Moor *et al.* (2015)
What are the key messages we need to communicate to the public about shifting distribution of marine and terrestrial species? How do we communicate them effectively? **ECO**	Creating opportunities for respectful dialogue between scientists and the public Improving ecological and science literacy	Jordan *et al.* (2009) Groffman *et al.* (2010)
How can people and communities contribute further to monitoring the impacts of changes in the distributions and relative abundances of species caused by climate change? **ECO**/**CONS**	Community-based observation systems	Higa *et al.* (2013) Chandler *et al.* (2016)

What is the effect of climate change on soil biodiversity, and how does climate change affect soil health and agriculture? **ECO**/**CONS**	SDMs and soil science	Hannah *et al.* (2013) le Roux *et al.* (2013)
How can marine spatial planning be reorganised to reconcile biodiversity conservation and food security? **ECO**/**CONS**	Adaptive management Restoration	Garcia & Rosenberg (2010) Rice & Garcia (2011) Sale *et al.* (2014)
What practical adaptations for agriculture, fisheries and aquaculture can be promoted to minimise the risks to food security and maximise the opportunities that are expected to arise from altered species distributions? **ECO**/**CONS**	Adaptive management Restoration	Bradley *et al.* (2012) Bell *et al.* (2013)
How will climate change impact the redistribution of disease-associated species and influence infectious disease dynamics? **ECO**	Host and vector SDMs	Rohr *et al.* (2008) Harrigan *et al.* (2014)
How can international environmental agreements that influence resource-management decisions incorporate local community observations and insights into their guidance and policy-making objectives? **CONS**	Evidence-based legal processes Multiple evidence-based frameworks	Tengö *et al.* (2017)