



# Animal culture impacts species' capacity to realise climate-driven range shifts

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Ecological predictions of how species will shift their geographical distributions under climate change generally consider individuals as machines that respond optimally to changing environmental conditions. However, animals frequently make active behavioural decisions based on imperfect information about their external environment, potentially mediated by information transmitted through social learning (i.e. culture). Vertical transmission of culture (between generations) might encourage conservative behaviour, constraining the ability of a species to respond, whilst horizontal transmission (within generations) can encourage innovation and so facilitate dynamic responses to a changing environment. We believe that the time is right to unite recent advances in ecological modelling and behavioural understanding to explicitly incorporate the influence of animal culture into future predictions of species distributions.

## Individuals are not machines

Efforts to improve forecasts of species distributional range shifts under climate change scenarios are progressing rapidly as more detailed biological information is incorporated and dynamic process-based approaches are applied (Fordham et al. 2014, Ehrlén and Morris 2015, Zurell et al. 2016). One aspect that is currently receiving a great deal of attention is the development of the conceptual basis and methods to incorporate biotic interactions into distribution models (Araújo and Luoto 2007, Kissling et al. 2012, Wisz et al. 2013). Generally, co-occurrences of species are used as proxies to describe where the target species is limited by availability of food (Araújo and Luoto 2007), habitat (Kissling et al. 2010) or the presence of a competitor (Algar et al. 2013). Despite this progress, we are missing a satisfactory understanding of how and why biotic interactions occur. We suggest that macroecology can benefit greatly by exploring the underlying behaviour governing species interactions, and other population processes (e.g. dispersal), which are closely linked to species distributions. Following the lead of invasion, urban and conservation ecology (Sutherland 1998, Sih et al. 2011, Sol et al. 2013, Greggor et al. 2014, Wong and Candolin 2014), it is time for explicit consideration of the role for behaviour in macroecology.

## The role of behaviour in species distributions

Behaviour influences species distributions by mediating ecological dynamics (Sutherland 1998, Reed 1999, Sih et al.

2011, Sol et al. 2013, Greggor et al. 2014) through decisions on what to eat (Van Schaik and Knott 2001, Slagsvold and Wiebe 2011, van de Waal et al. 2013), how to interact with conspecifics and other species (Suttle et al. 2007, Walther 2010, Bull et al. 2013, Sol et al. 2013), and when and where to move (Helfman and Schultz 1984, Colbeck et al. 2013, Mueller et al. 2013). For instance, according to lab-based thermal tolerance experiments, some regions in which ectothermic species are distributed are hotter than the critical thermal maxima of those species and therefore should be uninhabitable (Sunday et al. 2014). One hypothesis to explain this contradiction is that the animals respond to information in their environment and escape dangerous heat through behaviours that include burrowing, shade use and evaporative cooling (Sunday et al. 2014). Therefore, it is clear that the inclusion of behaviour in forecasts of species distributions and vulnerabilities has the potential to improve forecasts of climate change impacts (Reed 1999).

Understanding these behaviours and how they affect species distributions requires us to consider the underlying process of decision-making that precedes any observable behaviour. Decisions are considered to be made based on 1) internal motivation and 2) information from the external environment (Krebs and Davies 2003). For example, if an animal experiences hunger it will tend towards deciding to search for food; however, the initiation of this behaviour will also be influenced by the presence of predators in the external environment (e.g. the 'landscape of fear' effect; Hernández and Laundré 2005, McComb et al. 2011). This process assumes that species make optimal decisions guided by regular and accurate sampling of their local environment,

and may well be captured implicitly in existing species distribution models (SDMs). In other words, species are assumed to act as perfectly programmed machines. But how realistic is this assumption?

While it provides a useful starting point, evidence from ecology, economics and psychology demonstrates that animals frequently make active behavioural decisions based on imperfect information about their external environment (Schmidt et al. 2010, Nicolaus et al. 2016), which can result in a behaviour that is suboptimal for maximising fitness. Humans and non-humans alike frequently violate outcomes predicted by optimal decision-making models for a variety of potential reasons (De Martino et al. 2006, Pothos and Busemeyer 2009, Kalenscher and van Wingerden 2011). This is particularly true in novel situations, such as urban environments, where stimuli close enough to those found naturally elicit a behavioural response that is suboptimal in that context (Sol et al. 2013, Greggor et al. 2014). For example, male beetles were observed attempting to copulate with discarded beer bottles because the colour and texture mimics the female beetles (Gwynne and Rentz 1983). Perhaps some of the least considered constraints on behavioural repertoire are those imposed by animal culture (but see Whitehead et al. 2004).

With this review, we hope to encourage macroecologists to explicitly consider behaviour at the intersection of evolution and ecology in the pursuit to understand species distributions. Specifically, we focus on the extent to which decisions driven by non-human animal culture (hereafter shortened to 'animal culture') could impact the capacity for species to acclimate and adapt to climate change and to realise predicted future range shifts. We consider the implications of animal culture on conservation strategies in a changing world and outline potential ways to integrate animal behaviour into a dynamic SDM framework.

## Impacts of animal culture on species range shifts

We use the definition of culture offered by Rendell and Whitehead (2001): 'information or behavior – shared by a population or subpopulation – which is acquired from conspecifics through some form of social learning', which can occur either across or within generations (Whitehead et al. 2004). The existence of culture in animals has been hotly debated over the last decade, but by the definition above, is now largely accepted to be present across a diverse array of taxa that include fishes, reptiles, birds and mammals (Laland and Hoppitt 2003, Laland and Janik 2006). Indeed it has already begun to be recognised that animal culture is important enough to warrant consideration during the design of conservation measures (Convention on Migratory Species 2014).

Culture is thought to have evolved as a highly adaptive strategy that can allow individuals to circumvent costly trial-and-error learning by efficiently transferring valuable information between conspecifics. Transmitted behaviours are involved in many ecological processes including foraging (Mann et al. 2012, Allen et al. 2013, Mann and Patterson 2013), mating (Freeberg 2000, Wong and Candolin 2014) and migration (Whitehead et al. 2004, Clapham et al. 2008,

Whitehead 2010, Mueller et al. 2013). Such a system is particularly advantageous in a moderately stable environment. However, the continued effectiveness of culture as a strategy for enhanced survival in an era of rapid environmental change is questionable. One possibility is that culture will create 'ecological traps' that doom species to extinction (Schlaepfer et al. 2002). Alternatively, social learning could greatly increase the potential for species to avoid detrimental changes through the rapid transmission of individual innovations (Greggor et al. 2014). We discuss these options below and consider how they could affect the capacity for species to realise range shift forecasts derived from SDMs under scenarios of climate change.

## The potential danger of out-dated information

Vertical cultural transmission, where a behaviour is learnt from a previous generation, is found in a surprisingly wide variety of species (Carroll et al. 2015). Perhaps the most clearly relevant example of vertically transmitted culture for realising forecasted species range shifts is long-distance movement. Established migration routes transmitted through social learning across generations have been observed in some species of birds (Mueller et al. 2013) and cetaceans (Rendell and Whitehead 2001, Whitehead et al. 2004, Rendell et al. 2010b, Carroll et al. 2015), and are likely to be present in other groups of animals. There is strong evidence that highly conserved annual movement routes between breeding and foraging grounds are transmitted from mother to offspring in southern right whales (Valenzuela et al. 2009, Carroll et al. 2015), humpback whales (Whitehead 2010), and Beluga whales (Colbeck et al. 2013). As environments become progressively less stable, genetic adaptation struggles to occur against a background of rapidly changing selection pressures. Therefore, in unstable environments, transmission of cultural knowledge across generations could prove a highly adaptive alternative. For whales, finding suitable foraging and nursing grounds in such large oceanic regions without received knowledge is expected to be extremely costly and lead to mortality (Whitehead 2007, 2010).

On the other hand, conserved decisions can prevent exploitation of new regions that arise in response to environmental change, and even become maladaptive if the conditions in the established areas degrade (Fig. 1; Whitehead et al. 2004). In this situation, culture can actively suppress acclimation to changing conditions because individuals are making behavioural decisions based on out-dated information (Whitehead and Richerson 2009). This effect can be viewed as an ecological or evolutionary trap whereby a behaviour that originally boosted fitness, and therefore spread throughout a population, becomes detrimental to survival due to rapid changes in environmental or biotic conditions (Schlaepfer et al. 2002).

It is not only movement that is important for species distributions. Cultural transmission of foraging behaviour can influence an individual's ability to obtain food in both established and novel environments (Allen et al. 2013). For instance, culture can be involved in learning to locate, use and sometime even to manufacture tools. Sea otters can learn how to use rocks and kelp to catch and process food

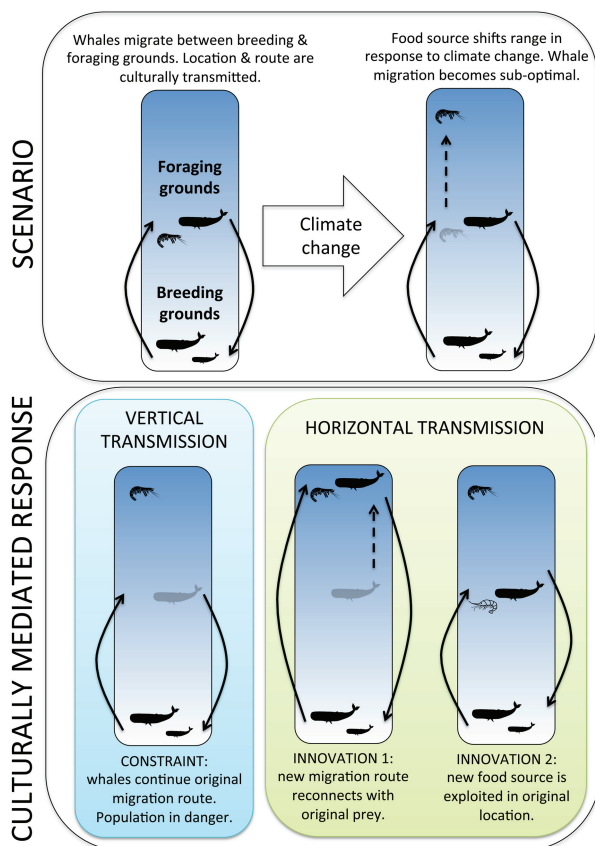


Figure 1. Schematic representation of the potential impact of climate change on species distributions and migration routes using whales as an example i.e. moving between breeding and foraging grounds. The top box shows a scenario where the main food source of the whales decreases in abundance due to climate change. The bottom box shows three possible responses, all of which are mediated by culture, with either negative (conserved vertical transmission) or positive (innovation followed by horizontal transmission) outcomes.

(Estes et al. 2003), a group of dolphins in Australia ‘wear’ sponges to protect their beaks while foraging (Mann et al. 2012, Mann and Patterson 2013), and meerkats appear to need an older demonstrator to learn to use novel food sources (Reader and Biro 2010). The degree to which these foraging behaviours are conserved (i.e. the rate at which they ‘mutate’) could have a direct effect on the potential for populations to shift into novel regions under climate change. For example, the forecasted presence of nutritionally suitable food in a new area is meaningless if the individuals predicted to move there are constrained to forage in a particular way owing to cultural norms.

Killer whales (orcas) offer a striking example of the power of cultural constraint (Riesch et al. 2012). Following capture and captivity, three individual killer whales from a population that specialised on marine mammals did not eat fish that were offered as food. These fish were known to be suitable nutritionally because they comprise a principal food source in other killer whale populations. As a result of this suboptimal decision to not eat fish, one individual starved to death. Therefore, constraints imposed by vertical cultural transmission can be extremely influential and could have

disastrous consequences for species attempting to cope with rapid environmental change.

## Grasping new opportunities

Contrary to vertical transmission, horizontal cultural transmission between individuals of the same generation can facilitate spread of individual innovations through a population. Where innovation leads to improved individual and population survival probabilities, theory suggests that horizontal transmission can accelerate acclimation to changing environmental conditions through space and time (Fig. 1; Whiten et al. 1999, Whitehead et al. 2004, Rendell et al. 2010b, Whitehead 2010, Greggor et al. 2014). In addition to aiding species persistence in novel environments, these processes could diminish the need for a species to shift its distributional range in the first place. Foraging innovations – development of a new behaviour not previously in a species’ repertoire – were observed to spread through humpback whale and killer whale populations at times when the abundance of their primary prey had decreased (Estes et al. 1998, Allen et al. 2013). Without such behavioural plasticity and social learning skills, these species might have been forced to shift distribution to track their original prey, potentially encountering further detrimental conditions.

Changes to species distributions also open up the possibility for cultural exchange between populations that would not previously have come into contact. Strong evidence for the possibility of such an exchange via horizontal transmission of movement behaviour amongst individuals is found in fishes (Brown and Laland 2003). Transplant experiments with the coral reef fish French grunts *Haemulon flavolineatum* demonstrated convincingly that nightly migrations to spawning grounds were learnt from conspecifics in the population (Helfman and Schultz 1984). Social learning of these routes is thought to increase fitness because it allowed individual fish to acclimate to new environments by learning from older conspecifics, and it prevented ‘stragglers’, which could become targets for predators (Helfman and Schultz 1984). In another example, two killer whale individuals of the captured ‘mammal-eating’ group discussed in the previous section, did accept and eat fish within 24 h of being housed with conspecifics from a fish-eating culture (Riesch et al. 2012). Therefore, population level range shifts might circumvent problems caused by constrained migration routes because shifting populations could learn from resident conspecific populations.

However, for many species range shifts we might reasonably assume there are no individuals of the target species in the novel region from whom to learn. In this case, innovation must necessarily precede behavioural transmission (Fig. 1). Figure 1 illustrates two potential innovations in foraging (Allen et al. 2013) and movement that could be horizontally transmitted and subsequently increase survival of whale species following a climate-driven shift in their food source. The potential to innovate in the context of biotic interactions could prove a distinct advantage because novel predators, parasites or competitors could be encountered as species respond to climate change idiosyncratically, reshuffling the species assemblage (Keith et al. 2009, 2011b).

In this case, additions to the behavioural repertoire will not only allow new resources to be exploited but will represent an essential transition to ensure species survival.

Possessing the behavioural flexibility to innovate has been linked to habitat generality, which together are likely to provide a distinct advantage for species introductions outside of their current range (Sol et al. 2005, Overington et al. 2011, Phillips and Suarez 2012). The relative trade-off between species where each individual needs to innovate compared with a combination of innovation and social learning is unclear. If an innovation is able to spread through a population via social learning, an advantage may be conferred on that species because only a few individuals might bear the risks associated with trial-and-error tactics on behalf of the wider population (Whitehead 2010). On the other hand, if innovations require active teaching for other individuals to learn effectively, this will commonly confer a cost on the teacher (Thornton and McAuliffe 2012).

Behavioural plasticity varies amongst species, affecting their propensity to innovate, learn, and subsequently survive in changing environments (Sol 2003, Phillips and Suarez 2012). On the flip side, an inability to acclimate through these behavioural mechanisms can greatly increase vulnerability to extinction (Reed 1999). Beyond species, it has also been suggested that there are differences in the potential for horizontal transmission within different physical realms. For instance, the potential for tool use is hypothesised to be higher in terrestrial environments because marine systems constrain body plans, properties of the water limit manipulative physical movements, and the vastness of the oceans limits opportunities for conspecifics to come into contact (Mann and Patterson 2013). However, empirical support for this hypothesis remains unclear.

### Behavioural diversity – evolutionary stable strategies for social learning

Taxa, functional groups and genes are the units of conservation, with efforts directed at maintaining their diversity. However, the conservation of behavioural diversity has received much less attention, especially beyond the cetacean literature (Sol 2003, Whitehead et al. 2004, Whitehead 2010, Wong and Candolin 2014). We assert that this is a substantial oversight because of the importance of behavioural plasticity for species survival in a changing world (Sol 2003, Sih et al. 2011, Phillips and Suarez 2012, Wong and Candolin 2014). Individual variation within species is also likely to be important to maintain behavioural diversity. Individuals exhibit distinct repeated characteristics of behaviour, or ‘personalities’, that describe their propensity to explore, innovate and socialise (Wolf and Weissing 2012, Canestrelli et al. 2016, Nicolaus et al. 2016). Recent evidence further suggests that personalities could change throughout an individual’s lifetime through epigenetics, in turn influencing ecological processes that determine species’ distributions e.g. bolder individuals may be more prone to disperse while shy individuals might be more sedentary (Canestrelli et al. 2016).

Losing a subset of personality types from a population could be detrimental (McDougall et al. 2006, Nicolaus

et al. 2016). For example, inadvertently or not, captive breeding programmes might select for the least explorative personalities, which could ultimately reduce the success of reintroduction by limiting acclimation to the new environment (McDougall et al. 2006). However, we note that for behavioural diversity to be important in species survival, group selection must be accepted as a possibility. Although contentious (Wilson 1983), empirical evidence suggests group selection can operate when behavioural traits are heritable (Pruitt and Goodnight 2014).

Theoretical work that explicitly simulates innovation, social learning, and decision-making amongst individuals within a population suggests that a mixture of personalities and learning style is the best evolutionary strategy for a species in a changing environment (Lehmann et al. 2010, Rendell et al. 2010a). Tournaments whose (human) entrants were required to design algorithms of social strategies to maximise ecological success under various scenarios, including changing environments, suggested that the best strategies rely on a mix of individuals learning primarily through vertical and horizontal transmission, combined with a limited number of innovators i.e. trial-and-error learners (Rendell et al. 2010a). However, the specific advantages of different algorithms depend on the amount of temporal and spatial autocorrelation in environmental conditions. Therefore, evolutionary stable strategies (ESS) emerge with specific ratios of behavioural types or learning styles dependent on the broader context (Rendell et al. 2010a, b).

These theoretical hypotheses are supported by empirical evidence. The survival of bird individuals with different personalities is a function of population density: at low densities more explorative individuals outperform the more conservative individuals but the situation is reversed as density increases (Nicolaus et al. 2016). Dolphin ‘spongers’ – individuals who use sponges to protect their beaks – and non-spongers co-occur in the population, with individuals sticking to their strategy. It is hypothesised that this mix of strategies is evolutionarily adaptive for the species because it reduces competition and expands the available niche that can be exploited by the population (Mann et al. 2012). This observation raises the idea that even when behavioural diversity is not strictly necessary to survive, it can lead to greater abundance of a species during range expansion or shift and potentially reduce its vulnerability to environmental disturbances.

### Understanding and forecasting the influence of social learning on species distributions

A wide variety of models are used to explore ecological processes and predict species distributions, many of which have been applied in the context of conservation strategies (Zurell et al. 2016). These include models that are spatial or non-spatial; static or dynamic; deterministic or stochastic; and range across many temporal, spatial and ecological scales (Purves et al. 2013). One common way of categorising models is to group them into statistical and process-based (sometimes conflated with ‘mechanistic’) models – where the former derive from observed biotic relationships based on empirical data, and the latter are grounded in theoretical



understanding of underlying ecological processes. Although it cannot necessarily be assumed, process-based models should be more powerful for the purposes of biodiversity conservation, tending to have greater predictive power under environmental change (Cuddington et al. 2013).

It is clear that models seeking to incorporate changes in climatic suitability must consider both direct and indirect influences of climate change (Suttle et al. 2007). Direct influences include physiological responses of individuals to predicted changes in climatic conditions, whilst indirect influences may concern the effect of climate on other organisms that interact with the target species or climatic influences on human activity. In addition, the literature urges that consideration be given to the potential for feedback loops in dynamic ecosystems (Nicholson et al. 2009). Whilst it is common for stochastic models to be used in conservation management (Pouzols and Moilanen 2013), and frameworks for dealing with uncertainty in ecology are available (Regan et al. 2002, Kujala et al. 2013), process-based models that incorporate behavioural plasticity to explicitly inform the design of conservation under environmental change are yet to be developed.

To incorporate social learning, with special reference to culture, we propose starting from a broad platform that models behavioural plasticity. This extension would allow a single characteristic to capture both constraints and opportunities (Sol 2003, Wong and Candolin 2014), and ensure the model is generalisable across a wide variety of species and behavioural types. We envisage this model being implemented by coupling dynamic individual based models (IBMs), because innovation and social learning is ultimately generated and transmitted at the level of the individual (Kroeber and Kluckhohn 1952), with SDMs. In this way, we can scale up decisions based upon variation in behavioural plasticity to entire species distributions. In support of this approach, a seminal study on the dissemination of culture in humans (Axelrod 1997) showed that IBMs can be highly effective in capturing changing cultural dynamics. This model, together with those mentioned in the preceding section and others (Lehmann et al. 2010, Rendell et al. 2010b), provides a strong foundation for developing an IBM exploring the impact of behavioural plasticity amidst spatially explicit environmental change informed by realistic climatic models. The protocol to adapt, design and describe IBMs proposed by Grimm et al. (2006) offers a useful framework around which to structure the model.

In particular, IBMs must explicitly incorporate: 1) processes and 2) input variables (Grimm et al. 2006). For the purpose of incorporating behavioural plasticity, we interpret these as 1) innovation, learning, decision-making, and physical response, and 2) behavioural plasticity and trends of environmental change. We show schematically the key steps in combining these two models in Fig. 2. Using this generalised framework, we outline below how to test the principles put forward in this paper on the ability of horizontal or vertical cultural transmission to influence species range shifts in the face of environmental change: 1) define the current geographical distribution of individuals based on ecological occurrence data and relate this distribution to environmental conditions i.e. functional relationships. 2) Create decision rules governing individual movement

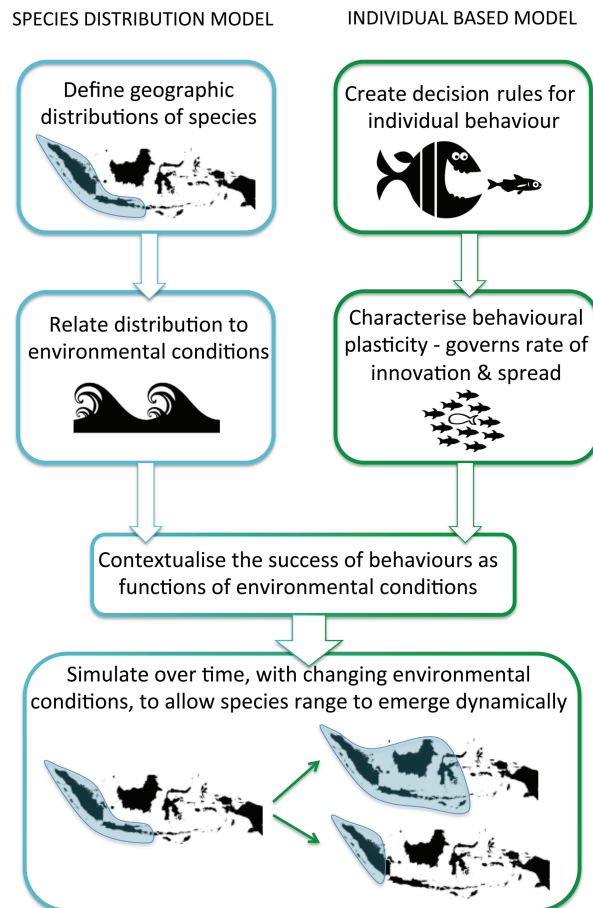


Figure 2. Flow chart for coupling species distribution and individual based models to simulate the movement of species over time in response to climate change. The model accounts for correlations between distribution and environmental conditions, and the potential for innovative or constraining behaviours. The simulations allow species distribution to evolve dynamically over time in response to changing environmental conditions, mediated through behaviour.

behaviour e.g. distance, direction, speed. 3) Characterise behavioural plasticity of individuals as a range that determines the potential and rate for innovations to arise and to spread throughout the population. Our working assumption in this paper is that behaviour transmitted vertically will generally be less plastic (although this assumption is easily changed). 4) Assign the success of different behaviours as functions of the environmental conditions. As the environmental conditions change in the current distribution, or new conditions arise following dispersal to new climate space, success rate of different behaviours can alter. 5) Simulate individual behaviour over time, in changing environmental conditions informed by climate models, to allow species distributions to emerge dynamically.

Model output would be subsequently compared against a version of the model that contains no behavioural element, to determine the extent to which culture could be an important consideration for the modelled species. The model could be explored theoretically, i.e. how far can distributions be altered by the inclusion of behaviour, and empirically if data were available to parameterise the behaviour.

## Designing interventions for cultured conservation targets

It has been clear for some time that conservation interventions can no longer be designed without accounting specifically for environmental change (Poiani et al. 2010, Bull et al. 2013). However, approaches for designing more dynamic interventions remain relatively undeveloped in terms of implementation (Runge et al. 2014). More traditional conservation interventions (e.g. protected areas) can be modified to account for environmental change. For instance, spatial planning of protected area networks can incorporate options for additional areas that allow for certain species to shift their range (Hannah et al. 2007).

Conversely, rather than extra protected area capacity, the focus could be to enhance the robustness of protected area networks to change by incorporating dispersal corridors, increasing resilience, and establishing core refugia for species that might have difficulty shifting their range (Malhi et al. 2008, Little and Grafton 2015). Alternatively, some authors have proposed mobile protected areas, which track species range shifts through time (Rayfield et al. 2008). However, such approaches rely heavily upon accurate projections of habitat suitability (Hole et al. 2011, Singh and Milner-Gulland 2011), and careful incorporation of historical trends and counterfactuals into the design and evaluation of conservation interventions (Ferraro and Pattanayak 2006, Bull et al. 2014, 2015).

To incorporate such complexity, enhanced ecological modelling approaches are increasingly important in designing conservation interventions that account for change. One way forward is to move towards process-based (as opposed to statistical) models, which allow species ranges to emerge dynamically. Because these models are driven by underlying ecological processes, rather than correlative relationships with environment, they are expected to improve prediction of species' responses to novel environmental conditions (Bauer and Klaassen 2013, Naujokaitis-Lewis et al. 2013, Purves et al. 2013). Unfortunately, process-based models often require more existing data to parameterise if they are to generate accurate projections, but these data are often scarce or non-existent. As a result, the use of decision-theoretic approaches from applied mathematics is also increasingly being explored (Martin et al. 2014). Runge et al. (2014) suggest that where information is limited there are three options available: 1) investing in increased empirical knowledge; 2) designing and implementing interventions that account for uncertainty based upon best available current knowledge; or 3) increasing knowledge through carefully designed conservation interventions (i.e. adaptive management).

In this case, option 1) would require collection of primary behavioural data in the field through observation and field experiments. For this option to apply to macro-ecological and biogeographical scales, these data are needed from across large geographical extents to capture context-dependency. However, this option is not necessarily the best route for using limited resources to ensure robust conservation outcomes (McDonald-Madden et al. 2010). A compromise might be possible if we apply decision theory to efficiently prioritise data collection i.e. to establish which

new information is most useful for improving conservation interventions and most likely to lead to a change in management (Nicol and Chades 2012). Option 2) uses some of the aforementioned approaches that account for uncertainty and build in resilience as part of conservation planning. Option 3), adaptive management, is a popular idea in principle, but barriers still exist to its successful implementation in practice (Keith et al. 2011a).

In summary, the design of interventions for species under climate change scenarios that incorporate behavioural plasticity will require a balance of developing appropriate process-based models and obtaining sufficient data to parameterise those models. Assuming this as a prerequisite, we now discuss ways in which cultural interactions could potentially be incorporated into future conservation interventions.

## Identifying and implementing appropriate conservation actions

For the practical aspects of conservation planning such as where to site protected areas, we expect the incorporation of animal culture into conservation actions to make mainly quantitative differences. That is, culture will influence how many individuals shift their range, how far it is shifted, and when exactly the shift occurs. It is only in extreme cases that we envisage cultural considerations could qualitatively change the required conservation interventions. As such, it would primarily be a case of incorporating culture into existing and emerging approaches for designing conservation measures in a changing world (Whitehead 2010, Greggor et al. 2014).

In some cases it is clear that incorporating an understanding of animal culture into conservation measures could increase success. Mueller et al. (2013) report on a programme to release captive-bred whooping cranes that have had no opportunity to learn migratory routes through cultural transmission, and instead were 'taught' to migrate by humans in ultralight aircraft. The authors suggest that migration in whooping cranes depends upon social learning in addition to innate knowledge, and therefore in this case effective conservation required supporting the cultural development of captive-bred animals. Reviving lost cultural memory has posed a problem for reintroduction of captive bred alala (Hawaiian crow), which has been extinct in the wild for over a decade. Previous releases were unsuccessful because insufficient cultural transmission between individuals prevented the population from becoming adept at avoiding predation and other necessary behavioural responses. Consequently, the current focus for the captive populations is to develop 'authentic crows' through active teaching (van Dooren 2015). Important cultural memory can also be lost without total extinction in the wild. Baleen whale population sizes were drastically reduced by commercial whaling and consequently, suitable areas of their historic range are no longer used even following population recovery (Clapham et al. 2008). Fortunately, through harnessing positive cognitive cues it might be possible for the species to recolonise these areas and revive cultural memory (Greggor et al. 2014).

Novel conservation strategies that capitalise upon an improved understanding of animal cultural norms could also be pursued. One consideration is the extent to which a given species can learn behaviour in the face of new threats or to keep pace with new opportunities arising, and transmit this behaviour to others (Sih et al. 2011). For instance, it might be that interventions prioritise conservation effort for populations of a species that exhibit cultural norms most likely to ensure survival, such as those populations within a migratory species that appear to be willing to change their route over those that are not. Or, if possible given intraspecific competition in the target species, interventions could be designed that encourage communication and dissemination of those cultural norms from one population to another. This could be achieved by periodic translocations of individuals within a managed metapopulation (e.g. see intervention to prevent genetic inbreeding in the Florida panther; Johnson et al. 2010).

Building upon the aforementioned examples of taught 'natural' behaviour (Mueller et al. 2013, van Dooren 2015), humans have also taught non-humans practices that they would not acquire in the wild that are then transmitted through imitation such as basic tool use in Japanese macaques (Iriki and Sakura 2008), or completely new methods for obtaining food sources in gorillas (Stoinski et al. 2001). This approach could feasibly form part of interventions that introduce behaviours to wild populations of certain species, allowing them to better adapt to predicted climate scenarios. Conversely, conservationists might seek to prevent cultural transmission of certain novel behaviours under environmental change because these might lead to undesirable effects on the wider ecosystem such as the spread of invasive species or declines in other species. For example, interventions could target black rat sub-populations that have learned to capitalise on new food sources or orcas that have switched to hunting sea otters (Estes et al. 1998) before such behaviour is passed on through social learning (Sol 2003). Of course, cultural interventions such as these would not only be challenging to design or even formulate, but would likely be controversial and potentially deeply unethical. Nonetheless, they are worthy of further exploration.

## Conclusion

Species distributions are not only limited by physiological tolerance but also by cognitive constraints, such as those imposed by cultural norms. However, we must keep in mind that unequivocal attribution of behaviours to social learning, especially when it is thought to be vertically transmitted, is not always possible due to the similar patterns of behavioural distributions that could be generated by genetic inheritance (Laland and Janik 2006, Mueller et al. 2013). Therefore, we must take care in assuming the appropriateness of conservation interventions aimed at social learning, and not at genetic adaptation. To begin to resolve the uncertainties around animal culture and species distributions, a broad research program is required. Below we include a list of some key outstanding questions. 1) Which of the factors that play a role in species geographical

distributions are influenced by animal culture? 2) How important is the influence of culture on species distributions relative to other underlying drivers, and for which species does it contribute significantly? 3) Does vertical cultural transmission always act to limit, and horizontal transmission always act to facilitate, the capacity of a species to respond to climate change? 4) How does the rate of climate change affect the strength of cultural constraints? Over what time scales will an over-reliance on out-dated information as a result of vertical cultural transmission lead to extinction? 5) What is the most effective way to incorporate culture into forecasts of species distributional change? 6) How do we most effectively design conservation interventions that account for animal culture?

In conclusion, understanding when decisions on movement are likely to be constrained or facilitated by culture might improve our ability to identify species that would benefit from 1) innovative interventions (Mueller et al. 2013), and 2) explicit consideration of 'adaptive behavioural diversity' (Rendell et al. 2010a) in conservation management; whilst also revealing 3) species with enhanced adaptive potential owing to their propensity for social learning. As a result, we believe the effect of animal culture on species distributional shifts under climate change is an interesting and potentially fruitful topic for macroecological research.

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