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The performance of protected areas for biodiversity under climate change

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Global environmental changes have been driving large-scale shifts in the distributions of species and in the composition of biological communities. This has thrown the continuing value of Protected Areas (PAs) into question, given that PAs remain static, whereas species move, and they are predicted to continue to move under future climate scenarios. We consider empirical evidence on the observed performance of PAs during the last 40 years of anthropogenic climate change. Despite some losses of populations and species, PAs have continued to accommodate many species, which have shifted to higher elevations, to polewards-facing aspects, and into cooler microhabitats within PAs as the climate has warmed. Even when species have declined in some PAs, they often remain more abundant inside than outside PAs. Furthermore, losses from some PAs are offset by increases in others. As species expand their ranges polewards across fragmented landscapes in response to climate warming, the majority are disproportionately colonizing PAs as they go. Hence, PA networks are acting as stepping-stones of suitable breeding conditions and facilitating range shifts, with many species remaining protected across PA networks as a whole. Finally, there is some evidence that appropriate management of PAs may be able to slow climate-related declines and accelerate expansions. The 40-year track record of species responding to environmental change in PAs suggests that networks of PAs have been essential to biodiversity conservation and are likely to continue to fulfil this role in the future. The challenge for managers will be to consider the balance between retaining current species and encouraging colonization by new species. *Biological Journal of the Linnean Society*, 2015, **115**, 718–730.

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INTRODUCTION

A cornerstone of conservation has been to establish Protected Areas (PAs; variously known as nature reserves, preserves, and National and Regional Parks), where the intention is to maintain conditions that will enable the species and biological communities that they originally contained to thrive. However, the distributions of species are dynamic and have become increasingly so over the past 200 years as they respond to land use change, pollution, the arrival of invasive species, climate change, and other anthropogenic drivers. Those few species that have not been impacted directly by these drivers of change will have been affected by the changing biological communities that they now experience.

Evidence indicating that widespread geographical range shifts are taking place in response to human-caused changes to the environment is increasingly strong (Mason *et al.*, 2015), thanks to a combination of observation records collated by a variety of recording schemes, notably the UK Biological Records Centre, and by more specific repeat surveys. The rates and directions of changes have been individualistic, with some species exhibiting collapsing distributions, whereas others (even within the same taxonomic group) have thrived and expanded their ranges. For example, some butterfly species in Britain have expanded their ranges rapidly in response to

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*Corresponding author. E-mail: chris.thomas@york.ac.uk climate warming, whereas others have declined (Warren *et al.*, 2001; Franco *et al.*, 2006). The majority of British spiders, grasshoppers, and ground beetles species have also moved northwards, although some have retreated southwards (Hickling *et al.*, 2005, 2006; Chen *et al.*, 2011a). British birds have shifted their distributions in multiple compass directions, albeit with an excess of movements northwards (Gillings, Balmer & Fuller, 2014). Furthermore, geographically widespread species have increased in some regions and declined in others (Fox *et al.*, 2014). This dynamism of species' distributions has proven challenging for conservation when species inhabit fragmented and short-lived successional habitats, and climate change now extends this challenge to the majority of species.

Because most PAs have fixed borders, there is concern that they may lack the flexibility to maintain populations of species whose distributions move in response to climate change and other environmental drivers (Peters & Darling, 1985; Heller & Zavaleta, 2009; Monzón, Moyer-Horner & Palamar, 2011). Indeed, modelling studies have shown that species are likely to move out of individual reserves with continuing climate change, potentially requiring additional reserves to achieve a given level of conservation success in the future (Araújo *et al.*, 2004; 2011; Hannah *et al.*, 2007; Leach, Zalat & Gilbert, 2013). Individual PAs have been predicted to gain or lose species or remain stable over time, although these predictions can be constrained by a lack of data on potential colonists from outside the study area (Leach *et al.*, 2013).

The body of modelling work assessing the potential impacts of climate change on the conservation status of species is growing. Modelling of Important Bird Areas (IBAs; not all of which are protected) in Africa, Europe, and Asia shows that almost all species are projected to have some suitable climate space within the network of IBAs in the future, even if some IBAs become unsuitable for individual species. In most cases, at least one IBA within the species' current range is predicted to remain suitable in the future (Hole *et al.*, 2009; Huntley *et al.*, 2010; Bagchi *et al.*, 2013). However, a much higher percentage of species are predicted to lose suitable climate space within the network than are predicted to gain suitable conditions. Species listed in Annex 1 of the Birds Directive in Europe were predicted to be those most affected by climate change, with the lowest predicted persistence in IBAs (Huntley *et al.*, 2010), although empirical studies have shown that these species have improved population trends in areas with more protected land (Donald *et al.*, 2007). In Finland, Virkkala *et al.* (2013) projected the future distributions of 100 birds of conservation concern and found that PAs are predicted to continue to protect suitable habitat for species preferring mires, marshes and arctic mountains, although the current network will not be sufficient for woodland birds.

For plants, PAs in the UK are predicted to protect more suitable climate space for bryophtes in the future than they currently do, although there is no overlap between the current and predicted future range for at least 25% of the species modelled (Anderson & Ohlemüller, 2010). Similarly, Thuiller *et al.* (2014) modelled the predicted future distribution of 2542 plants in the French Alps. Rare species and species of conservation concern were projected to experience less severe change than others and were also the most efficiently preserved by the current network of PAs. In Australia, the future representation of current environments (based on generalized dissimilarity modelling of vascular plants) in the National Reserve System is expected to be poor, although there is predicted to be a good representation of the range of projected future environments (Ferrier *et al.*, 2012). Modelling exercises such as these are extremely valuable for identifying the challenges facing PA networks, although the diversity of modelled outcomes leaves considerable uncertainty about the likely realized performance of PAs under climate change.

To complement the models, it is useful to assess empirical evidence concerning the recent performance of PAs, given that we have already experienced four decades of rapid anthropogenic climate change. In the present review, we address this issue, concentrating on the biological rather than legal or social utility of PAs. Data collated by the UK Biological Records Centre, partner organizations and internationally enable us to conclude that PAs remain essential to conservation strategies even though the compositions of species present within reserves, and their relative abundances, are changing.

ARE SPECIES ABLE TO SHIFT THEIR DISTRIBUTIONS WITHIN RESERVES?

Most species have localized distributions or spatial variation in population densities within the PAs that they currently occupy. Their densities vary from the micro- to the meso-scale (e.g. the locations where individual insect eggs are laid through to the elevational range of a species on a protected mountain). This provides opportunities for species to shift their distributions and abundance patterns to the most suitable locations within existing PAs, rather than shifting to other PAs. For example, populations could move uphill and/or to slopes facing towards the poles or into denser vegetation to escape higher summer maximum temperatures than they can tolerate (Suggitt *et al*., 2011). Similarly, they might move into shadier vegetation or hollows to reduce the likelihood of desiccation.

Perhaps fortunately, PAs across the world are often disproportionately found in mountain ranges and at relatively high elevations (Klorvuttimontara, McClean & Hill, 2011; Gillingham, 2013; Thuiller *et al*., 2014), and in the 'wastes of the north', although this is not always the case (Khan, Menon & Bawa, 1997). Large, mountainous PAs provide opportunities for species to take advantage of cooler conditions at higher elevations without being displaced out of the PA. Many mid-elevation bird species increased in abundances at higher elevations within the Monteverde Cloud Forest Reserve in Costa Rica (Pounds, Fogden & Campbell, 1999), a majority of geometrid moth species moved to higher elevations in Mount Kinabalu National Park in Borneo (Chen *et al*., 2009; 2011b), and amphibian and reptile species moved to higher elevations in Tsaratanana Reserve in Madagascar (Raxworthy *et al*., 2008). The same is true in the temperate zone, where small mammal and bird species have shifted elevations (both up and down) in Yosemite National Park in the USA (Moritz *et al*., 2008; Tingley *et al*., 2009), and montane plants have moved to higher elevations on mountain summits in PAs in Europe (Pauli *et al*., 2012). These studies have also all detected some species declines, and several regional and even species-level extinctions have been observed, and so the presence of a species in a topographically diverse PA does not guarantee survival. Nonetheless, the observed changes imply that many species will be accommodated by distribution changes within, rather than between, existing PAs, at least in the shorter term. Small PAs are less likely to retain areas with similar climatic conditions in the future (Loarie *et al*., 2009), and so they are less likely to retain the species that are currently resident than larger PAs as a result of a lack of temporal climate connectivity (Hodgson *et al*., 2009). Nonetheless, small-scale opportunities for local distribution and habitat changes may still exist in small reserves.

Thermal gradients are even steeper in relation to the aspect of mountain and hill slopes than to elevation, and this creates a diversity of microclimates even in relatively flat parts of the world (e.g. on south- versus north-facing slopes of river levees, and on small hills), as do differences in microclimates associated with vegetation height and cover (Thomas, 1983; Suggitt *et al*., 2011). The silver-spotted skipper butterfly, *Hesperia comma*, which was historically restricted to sparse vegetation on south-facing hillsides in lowland Britain, expanded its distribution during a period of regional warming to occupy increasing numbers of easterly, westerly and even shallow northerly-facing hillsides that would have historically been too cool for them to occupy (Thomas *et al*., 2001). This was associated with the butterfly's thermal threshold of approximately 24/25 °C, which is required for full activity and egg-laying (Davies *et al*., 2006). Most of these shifts took place within PAs as a result of the species' strong association with species-rich dry grasslands, the majority of which fall into PAs within the butterfly's British range (see below).

The option is available for individuals, populations, and even entire species to survive hotter conditions by shifting into cooler vegetation, given that summer thermal maxima may be 5 °C cooler under a woodland canopy than in an adjacent open habitat (Suggitt *et al*., 2011). Conversely, Davies *et al*. (2006) found that increased temperatures enabled *H. comma* to expand its local distribution into denser grasslands where less bare ground was available for adult thermoregulation because this was no longer required so frequently for the insects to become fully active.

An analysis of data based on counts of butterflies on transects (many of which are on PAs) in Britain and Catalonia, Spain, found that species did tend to move from more open to closed vegetation types under hotter conditions. This only represented a shift of 1.3% of individual butterflies for each degree of warming, presumably because they are limited by other traits or ecological constraints (Suggitt *et al*., 2012). This evidence suggests that the majority of species are not in the process of undertaking complete shifts in the type of vegetation they inhabit (i.e. from one biome to another), although a few species have undertaken major habitat shifts under recent climate warming (see below). On the basis of current evidence, we expect that most of these local (within PA) changes in habitat associations will be ecologically modest but thermally important; such as shifts from south- to north-facing hillsides in moorland vegetation (which may generate a mean maximum temperature difference of approximately 7 °C; Suggitt *et al*., 2011), or from shorter to taller turf within grasslands (which also generate steep thermal gradients; Thomas, 1983). Shifts along local moisture and desiccation gradients are likely to be equally important (Carroll *et al*., 2011; Maclean *et al*., 2012). These very local differences in temperatures over distances of centimetres to hundreds of metres are equivalent to the magnitude of an extreme climate change scenario by 2100, and hence microhabitat shifts provide opportunities for population survival in lowland as well as in topographically diverse, montane PAs. It should be noted, however, that species already occupying the coolest microclimates in a PA will not have the flexibility to shift locally into more suitable conditions.

CAN THE STATUS OF SPECIES BE RETAINED ACROSS RESERVE NETWORKS?

There is some suggestion that networks of PAs (i.e. the set of all PAs within a given region) are more resilient to climate change and can accommodate shifting distributions more effectively than unprotected land. For example, Gillingham *et al*. (2014) found evidence that PAs in Britain retained the highest abundances of butterflies, dragonflies and damselflies decades after their designation, even though many species in these taxonomic groups undertook major distribution changes during this period. The difficulty, however, is demonstrating whether this is a result of protection, *per se*. Gillingham *et al*. (2015) found some evidence that British birds and butterflies retracting towards the poles have survived better within PAs even once latitude and altitude were taken into account. This positive effect of PA designation was more important at lower latitudes, perhaps because these were the least climatically suitable areas, although another possibility is the stronger difference in habitat quality between PAs and non-PA land in England compared to Scotland. Similarly, Beale *et al*. (2013) found that population losses of savannah birds were greatest outside PAs in Tanzania, as a result of land use changes, whereas climate-related gains in distribution were greatest inside PAs, generating an overall better performance inside compared to outside the PA network. In Moreton Bay, Eastern Australia, protected reefs were found to be more resilient to flooding caused by extreme weather than fished reefs, possibly as a result of increased herbivory and coral recruitment (Olds *et al*., 2014). Although not explicity considering the effects of climate change, Magdaong *et al*. (2014) discovered that the coverage of living hard corals increased between 1981 and 2010 inside Marine PAs in the Philippines but did not increase outside them. This was despite coral bleaching events, and did not appear to depend on the age, size or level of protection of the Marine PA.

Two studies have quantified recent changes in the density of birds on PAs across Finland, finding that northern species have decreased in PAs, whereas southern species have increased, as predicted if they are responding to climate change (Kujala *et al*., 2011; Virkkala & Rajasärkkä, 2011). These studies do not compare the changes occurring within PAs with those occurring outside them but they do illustrate that changes in species composition have occurred within PAs, and that many species have increased across the reserve network (even if others have declined). More recently, Virkkala *et al*. (2014) found that Finnish PAs have maintained higher avian species richness than non-PAs, implying that PAs remain the best places to conserve species despite any declines that have occurred. Johnston *et al*. (2013) demonstrated that a PA network for birds in Britain has retained its conservation value in recent decades, and used models validated against observed trends to project that the PA network would continue to have high conservation value under future climate scenarios.

A commonly suggested conservation strategy for species experiencing negative impacts of climate change is to minimize threats posed by other environmental drivers (Heller & Zavaleta, 2009), and the value of PAs as a means to achieve this is illustrated empirically by the example of bird distribution changes in Tanzania (Beale *et al*., 2013). Similarly, populations of large-bodied temperate reef fish recovered over 20 years in reserves set up in Tasmania in 1991,resulting in an increased stability of biodiversity in those locations and less pronounced invasion by warm-adapted species (Bates *et al*., 2014). At a regional level, warm-adapted species were accommodated by colonizing areas outside PAs, whereas the colder adapted species performed better within them. This specific result will not necessarily be replicated in all environments (see below), although it indicates that PA management can strongly influence the relative performances of colder- and warmer-adapted species.

Given the nature of distribution changes, there is a clear need for these empirical assessments of the performance of PA networks to be carried out at continental scales. Empirical evidence is also lacking for most taxonomic groups. However, the tendency for terrestrial animal species (but not marine species, with little evidence for plants) to expand slightly faster at their leading (i.e. upper and polewards) range margins than to retreat at their trailing edges (Chen *et al*., 2011b; Sunday, Bates & Dulvy, 2012) implies that the transition to a new distribution may sometimes involve a phase of increased range size, which implies that representation across continental-scale PA networks could potentially be increased slightly rather than decreased in the coming decades.

CAN SPECIES USE RESERVES AS STEPPING-STONES AS THEY SPREAD INTO NEW REGIONS AND COUNTRIES?

Maintenance of the status of species at a continental scale requires colonization of new regions; maintaining strong representation on PAs requires species to colonize new PAs as fast as existing populations disappear from the PAs where they historically occurred. PAs may be particularly important in the colonization of landscapes dominated by human activities, where suitable breeding sites may be scarce and far apart.

Suitable habitats (and PAs) may need to be sufficiently concentrated and arranged as stepping-stones across fragmented landscapes to enable species to expand their ranges (Hodgson *et al*., 2011, 2012). Evidence for species using reserves as stepping-stones to facilitate spread into new regions comes from several studies.

In Britain, Thomas *et al*. (2012) found that 256 species across eight invertebrate groups disproportionally used PAs in newly colonized areas. For most of the species considered in that study, data came from records collected by volunteers through national recording schemes, collated by the UK Biological Records Centre. More detailed, repeat surveys of the same locations were available for seven species (five birds and two butterflies), with records being 14 times more likely to be within PAs than outside for the silver-spotted skipper butterfly *Hesperia comma* (Fig. 1), and strongly biased towards PAs for four of the other species. In a further study of British butterflies and odonates, Gillingham *et al*. (2014) found that some species were also significantly more abundant inside PAs in newly colonized parts of their range, where PAs had not been designated for them. Species that were disproportionately abundant on PAs in their core ranges were also relatively abundant on PAs in new regions, meaning that PAs have been particularly useful in helping a subset of PA-reliant species develop sizeable populations in new areas.

In addition, bird species that have colonized the UK from elsewhere in Europe have disproportionately established breeding populations in PAs (Hiley *et al*., 2013). Reliance on PAs declined significantly over time for three of six bird species as they subsequently colonized new locations within the UK. A similar pattern is observed within administrative districts within the UK; populations colonizing each new county tended to establish first in a PA, before spreading out into other sites (Hiley, Bradbury & Thomas, 2014). PAs were particularly important for natural colonists and did not fulfil the same function for species that have recently been either deliberately or accidentally introduced. Therefore, PAs provided a bridge head for species colonizing and spreading within Britain, before they expand into other locations in the surrounding landscape; without acting as conduits for the expansion of introduced species.

It is worth noting, however, that that reliance on PAs during range shifts may vary among regions and ecosystems: for 139 birds in Tanzania, colonization between 1960–1980 and 2000–2006 occurred preferentially in PAs (approximately 80% of colonizations were in squares with some PA) (Beale *et al*., 2013), whereas Bates *et al*. (2014) found that four range-shifting subtropical vagrants were only found in nonreserve sites in marine systems in Tasmania, perhaps as a result of biological resistance in PAs (where large-bodied species were present). Individual colonists also vary in their associations with PAs.

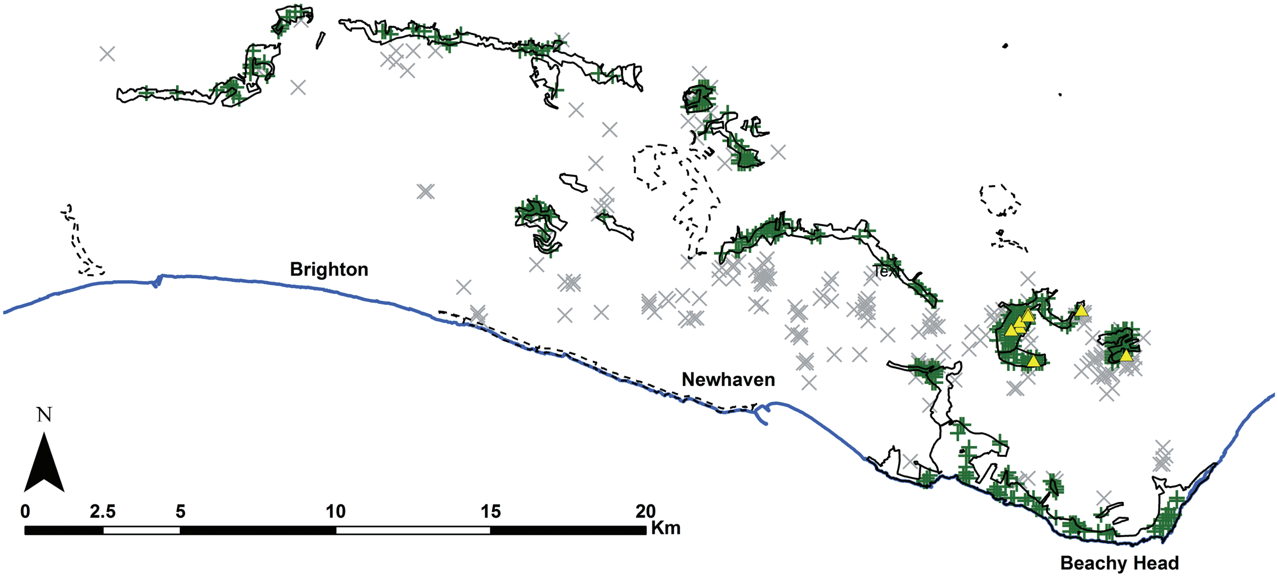

Figure 1. Use of Protected Areas (PAs) in southern England (lowest solid line shows the coast) during the range expansion of the silver-spotted skipper butterfly, in the county of East Sussex (*sensu* Thomas *et al*., 2012). Solid lines show boundaries of PAs that contain some potential silver-spotted skipper habitat; dashed lines show PAs without skipper habitat. Yellow triangles indicate skipper records 1950–1982 (original distribution, at the eastern end of the distribution), green plus symbol (+) records show post-1982 colonizations associated with PAs, and grey cross symbol (×) show post-1982 colonizations associated with non-PA land.

Although there is a general tendency for species with a strong reliance on PAs in their core ranges to remain strongly associated with PAs in new regions, not all habitat-restricted species are strongly represented in PAs, and some of these species may experience insufficient habitat availability to spread. In other words, the colonization of new PAs by many species provides strong support for the continued conservation value of PAs, although it does not constitute evidence that there is sufficient PA or habitat provision to enable all species to spread.

A few species have already undertaken major ecological and evolutionary shifts, generating completely unexpected range shifts, a phenomenon that might be expected to become more frequent under high levels of future climate change. The brown argus butterfly in southern England was strongly associated with species-rich dry meadows (calcareous grasslands), and was thus mainly associated with PAs, because its larval host plant, the rock rose *Helianthemum nummularium*, is mainly restricted to relatively short and warm vegetation on southerly-facing hillsides (Bourn & Thomas, 1993). Under warming conditions, the butterfly lost its need for southerly-facing slopes, although no-one predicted what would happen next to this 'specialized' insect. In warm summers, it was able to complete its larval development (two generations per year) in a wider range of sites and using host plants in the plant family Geraniaceae, which grew in places that were previously too cool for it (Thomas *et al*., 2001; Pateman *et al*., 2012). This resulted in a major habitat shift, such that the butterfly now exploits sandy soils, parks, gardens, rough ground, and even field margins, wherever the wild geraniums grow. Although this insect previously faced a highly fragmented landscape of calcareous grassland remnants, by exploiting new habitats, the butterfly was able to expand its range polewards extremely rapidly, and predominantly colonized non-PA land. This rapid expansion was assisted by the fact that it undertook an evolutionary switch; female butterflies in the northern, expanding part of the range favour *Geranium* plants for egg-laying (Thomas *et al*., 2001; Hanski, 2011; Bridle *et al*., 2014). Other species, notably wing-dimorphic bush crickets, now exhibit an increased frequency of highly dispersive, long-winged individuals near their expanding range boundaries, accelerating their rate of expansion (Thomas *et al*., 2001; Simmons & Thomas, 2004; Hill *et al*., 2011). In both cases, evolutionary feedbacks have 'defragmented' the landscape from the perspective of these species, reducing their reliance on high-quality stepping-stones of PA land to spread. However, most species have not achieved such changes. From a conservation perspective, it should not be presumed that a species is going to do so.

CAN THE MANAGEMENT OF PAS HELP REDUCE LOSSES AT TRAILING EDGES, AID ADVANCES AT LEADING EDGES, AND ARE THEY MUTUALLY EXCLUSIVE?

Monzón *et al*. (2011) identify nineteen species of animals listed as extinct or extinct in the wild as a result, at least in part, of climatic factors. Other species have died out from parts of their distributions (Thomas & Williamson, 2012), including in reserves. This raises the issue of the management of PAs, which could potentially be used to retard climate-related declines and/or accelerate expansions into regions that species must reach if they are to survive the 21st Century and beyond. Almost any management that has achieved conservation success (or failure) is relevant here, given that anthropogenic climate change has been altering the climate everywhere over the last four decades. Hence, the following examples are simply illustrative. PA designation can encourage conservation management; PA sites are more likely to be managed for wildlife than non PAs in Britain, for example (Lawson *et al*., 2014). Although intensive management might appear to be a rather European perspective, management of many processes are commonplace across the world's PAs. Under climate change, adaptive management of large vertebrates (affecting vegetation structure for everything else), fire and ground water regimes may be important, particularly given the changes in microclimate under different heights and densities of vegetation (see above). We already manage these processes, and will be faced with difficult decisions as to whether and how we should alter this management in the future.

A recent meta-analysis of the effects of climate change on terrestrial and freshwater populations found that indirect, biotic mediators, such as predation, prey availability, and diseases, were particularly important, especially for species at higher trophic levels (Ockendon *et al*., 2014). The implication of this is that management of biotic interactions might help to mitigate the impacts of climate change for some species; management that decreases one pressure might be expected to increase resilience to other pressures (Pearce-Higgins, 2011). Management within PAs could be adjusted to reduce losses at the trailing edges of species' ranges, allowing them to persist for longer than might otherwise be expected, potentially indefinitely. For example, a key food source during the breeding season for the golden plover *Pluvialis apricaria* at their equatorwards range boundary is adult craneflies (Diptera: Tipulidae) (Pearce-Higgins *et al*., 2010). Re-wetting the peat that cranefly larvae inhabit (by blocking drainage channels) has increased the number of adult craneflies available (Carroll *et al*., 2011), which might be expected to help the golden plover persist in the face of climate change, with the added benefit of decreasing the loss of CO_2 to the atmosphere (Holden, 2005). Ecosystem management to maintain this simple food chain has considerable potential. Similarly, management of vegetation characteristics has the potential to compensate for the effects of climate change for four cold-adapted birds in Central Europe (Braunisch *et al*., 2014), although no single management option is expected to achieve full compensation.

Alternatively, management within PAs might be employed to facilitate the expansion of species into new areas. For the silver-spotted skipper butterfly, there is evidence that PAs under primary conservation management (with the aim of maintaining short sward chalk grassland, which is home to many butterfly species in addition to *H. comma*) were more likely to be colonized than sites under voluntary management via schemes where the landowner was paid to carry out certain conservation actions. In turn, these were better than unmanaged sites of the same basic vegetation type (Lawson *et al*., 2014). Conservation action also increased the survival rate of existing *H. comma* populations both inside and outside of PAs. Although this analysis represents a retrospective on the impacts of past management, it is also possible to develop management scenarios for the future. For example, of three management scenarios modelled for future effectiveness under climate change in the Écrins National Park in the French Alps, the current annual grazing and mowing regime was predicted to result in an upwards shift of the treeline and understory species of 600 m; intensification of pasture use constrained the ability of tree species to colonize new areas, and abandonment of management resulted in faster colonization but lower local diversity at low-mid elevations (Boulangeat *et al*., 2014).

Management for one or a few species may be detrimental to others. Davies *et al*. (2006) found that, although population trends of eight British butterflies tended to be positive on biologically-designated Sites of Special Scientific Interest (SSSIs; IUCN level IVprotection), four of the species maintained higher populations on SSSIs recorded as being in ‘unfavourable condition’ (based principally on the vegetation characteristics) than on ‘favourable’ SSSIs. Thus, increasing the species associated with favourable vegetation condition may come at a cost to other butterfly species. Reserve managers will have to balance these conflicting objectives when designing their management plans.

Nowhere is this decision harder than when trying to reconcile the needs of expanding and contracting species in the same PAs, where the survival of potentially-retreating species may be favoured by a different management regime than one that favours the establishment of a new colonist. The Tasmanian reefs described above illustrate such a conflict, where the maintenance of large populations of temperate fish in PAs apparently slowed or prevented the establishment of species associated with warmer waters (Bates *et al*., 2014). A common suggestion is that we should maintain habitat heterogeneity to solve this problem, and buffer populations against climatic extremes (Heller & Zavaleta, 2009; Hodgson *et al*., 2011). UK butterflies, particularly those at their range margins, had dampened population dynamics, and perhaps therefore reduced likelihoods of extinction, in sites with a more heterogenous habitat, suggesting the potential value of this approach (Oliver *et al*., 2010, 2014). Buffering from weather-related population declines may also be achieved by reducing fragmentation. Newson *et al*. (2014) found that climatic impacts on populations of some woodland bird species in the UK were stronger at more isolated sites. Topographical and vegetation heterogeneity appears to be a widespread driver of species richness (Stein, Gerstner & Kreft, 2014), and so conservation actions aiming to maximize heterogeneity should also protect the largest possible number of species. However, only some components of heterogeneity can be manipulated, and this is not necessarily the ideal strategy for all PAs, where increasing heterogeneity results in less total area of each habitat type. Hence, management depends on the regional context. Warm-adapted fish are well catered for on heavily-fished reefs outside PAs in Tasmania, and so the priority inside PAs lies with the temperate species. In addition, management priorities could change over time, such that, when retracting species move away from a PA, management might safely be changed to encourage colonization of expanding species (Hole *et al*., 2011).

CAN EXISTING PAS BE USED TO RECEIVE NEW SPECIES THROUGH ASSISTED COLONIZATION?

For cases where *in situ* survival is impossible for a species despite management, and where there is no capacity for a species to spread to new locations via a string of PAs, translocation may need to be considered (Hoegh-Guldberg *et al*., 2008). This is rarely going to be the preferred option, given that management and stepping-stones of habitats also have the potential to benefit nontarget species. Nonetheless, translocation will most likely become an increasing feature of climate-change conservation over the coming century, and has already been predicted to be an effective management option for more than one species

(Bonebrake *et al*., 2014; Parmesan *et al*., 2014). A major question is where individuals should be released (Thomas, 2011), given the fear that the release of new species might hasten the demise of those that were previously present (Ricciardi & Simberloff, 2009). This would be a particular issue for sites and regions that contain local endemics, although most of the world supports very few local endemics because a high proportion of the planet's small-range species are concentrated into a small fraction of its land surface.

In 2000, Willis *et al*. (2009) translocated female marbled white (*Melanargia galathea*) butterflies to beyond the northern edge of their former range boundary in Britain. The aim was to determine whether this could help the species track climate change, given that the then northern edge of its distribution was constrained by a geological/ geographical barrier. The population grew rapidly, with no observed negative impacts on other species, and is still extant in 2014, establishing that the species' distribution was lagging behind climate change. The release site was a SSSI, indicating that this PA, at least, was suitable for assisted colonization. This is not the only example. The endangered conifer *Torreya taxifolia* has been planted to the north of its native range in the USA, including in at least one local reserve, although it may take centuries to determine whether a self-sustaining population has been achieved (Schwartz *et al*., 2012). Furthermore, Chinese scientists have successfully translocated orchids to higher elevations within a PA (Liu *et al*., 2012). Although this topic remains controversial, it could become an increasingly important strategy for PAs in regions that either lack or have lost endemics, which in itself is likely to be more common in the future.

CONCLUSIONS

Emerging evidence suggests that PAs are likely to continue to have high conservation value in the future, given their performance over the past 40 years of anthropogenic climate change. Populations of (rare) species are normally larger in PAs, some species have survived better in them as a result of protection from deleterious land use changes elsewhere, and many species have disproportionately colonized new PAs as they expand into new regions. There is also scope for biodiversity-oriented management and habitat creation to maintain existing species and/or facilitate the arrival of new species, and the possibility of introducing additional threatened species that cannot reach them unaided. Thus, PAs appear to be set to continue to deliver high biodiversity benefits, even if the relative abundances and identities of the species present changes. Regulatory ecosystem services provided by PAs may also continue to operate despite a changing biota (Eastwood *et al*., 2013). Empirical evidence, however, remains sparse. For example, the consequence of climate change for the representation of species in lowland tropical rainforest PAs is unknown.

PAs are, of course, not a panacea for conservation under environmental change. Montane forest endemics will be at risk of extinction if temperatures rise and moisture levels drop, and coral reefs may eventually collapse through warming and acidification, regardless of PA status and protection from other threats. These sorts of challenges may require new thinking. It is likely that we are at the beginning of a new period of major ecosystem management and engineering, aiming to achieve multiple biodiversity and ecosystem goals, including the storage of carbon. In Britain, management is already attempting to restore the historical hydrology to peat bogs that humans drained in the past. If rainfall decreases, we might have to decide whether we will deliberately pump water into these ecosystems to maintain their carbon stocks and associated biodiversity. In the lowlands of Britain, the Royal Society for the Protection of Birds and others have already deliberately created new wetlands (partly to mitigate against the inevitability of habitat loss associated with climate-driven coastal retreat) and heathlands, both of which have been colonized by species that are expanding their ranges (RSPB, 2010). Large herbivore numbers could be increased or decreased by management to maintain different types of vegetation structure; drying and dying forests could be irrigated to save endemic species; and deep cold water could be pumped onto coral reefs during El Niño peak temperatures to prevent bleaching. We are not saying that this is a desirable state for conservation, or for the planet as a whole. However, we will increasingly face difficult management decisions that have no historical precedent.

Conservation actions under climate change will need to facilitate the natural colonization of new areas as they become suitable for range expanding species, at the same time as also mitigating the effects of change for species with nowhere to move to. With these competing objectives in mind, it is important to identify conservation actions that have a good chance of remaining useful in the future, or that provide positive outcomes for a number of different objectives. This may include protecting landscapes with topographical diversity, managing for habitat heterogeneity, facilitating links between low and high elevation reserves, and translocating species when all else fails. Modelling studies have shown that planning for climate change when designing reserve networks should result in better conservation outcomes in the future for fish (Bond, Thomson & Reich, 2014), as well as better temporal connectivity of suitable conditions within reserves (Game *et al*., 2011; Makino *et al*., 2014) and better spatial connectivity between reserves or other suitable habitats (Hodgson *et al*., 2011, 2012; Makino *et al*., 2014). Accordingly, some countries are beginning to plan for climate change when considering their national reserve networks (e.g. Australia: Dunlop *et al*., 2012; Ferrier *et al*., 2012). Some reserve managers include adaptation to climate change in their plans and consider the wider reserve network (MacGregor & van Dijk, 2014), and species distribution models could be employed to identify key locations for new PAs that might increase the effectiveness of the network in the future (Vos *et al*., 2008; Hole *et al*., 2011).

Disproportionate colonization of PAs by colonizing birds, butterflies, odonates, and other invertebrates suggests that a PA network approach will be valuable. In addition, a disproportionate representation of both disappearing and novel climates in PAs in some areas (Wiens, Seavy & Jongsomjit, 2011) should help to both retain retracting species and encourage colonization by expanding species. However, the total land area and conservation effort required to deliver a given conservation target will almost inevitably be larger when species are on the move because sufficient high quality habitats are required to maintain species not only where they currently occur, but also in all places along the route to their new distribution (Hodgson *et al*., 2012). There is some suggestion from the modelling community that selling PAs once species have moved away and reinvesting the capital released in new PAs might achieve more favourable conservation outcomes, particularly at lower budgets (Alagador, Cerdeira & Araujo, 2014). However, the model employed in that analysis did not account for the actual or opportunity cost of maintaining suitable habitat outside PAs (e.g. retaining undisturbed, low-fertility soils), or the costs of recreating such habitats subsequently, making them available for designation in the future. We therefore suggest that this dynamic approach to land designation is unlikely to be viable in countries with a high pressure on land use or low financial capacity to restore habitats.

PAs may fail legally if they no longer contain the entities that they were gazetted to protect (Mascia & Pailler, 2011). However, provided that protection follows species (or their abundances), it is likely that many PAs may retain their conservation status because they will gain protected entities (new species, or increased abundances of some species that are already present), even if they lose others that were previously present (Johnston *et al*., 2013). In conclusion, most rare and threatened species have continued to require PAs and the habitats they contain over the last 40 years of anthropogenic climate warming. There is no evidence that this need has reduced in recent years, or that it will diminish in the future. Hence, a PA approach will remain essential if we are to maintain *in situ* populations of species.

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