Active Management of Protected Areas Enhances Metapopulation Expansion Under Climate Change

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Abstract

There is a need to adapt biodiversity conservation to climate change, but few empirical studies are available to guide decision-making. Existing networks of protected areas (PAs) have been preferentially colonized during species' range expansions, but this could be due to their original habitat quality and/or to ongoing management activity. Here, we examine how PA status and active conservation management have influenced the range expansion of a butterfly *Hesperia comma* through fragmented landscapes. PAs under active conservation management were over three times more likely to be colonized than unprotected, unmanaged sites of the same basic vegetation type. Conservation action also increased the survival rate of existing populations inside and outside of PAs. We conclude that PAs facilitate range expansions by preventing habitat degradation and encouraging active conservation that improves habitat quality, and that conservation interventions on nondesignated sites also have a role to play in adapting conservation to climate change.

Introduction

Species are responding to climate change by shifting their geographic distributions (Chen *et al.* 2011), but range expansions may be retarded or prevented by a lack of habitats available to colonize (Warren *et al.* 2001; Hill *et al.* 2002). Conservation strategies to preserve biodiversity in the face of global warming may aim to secure the survival of extant populations while helping species to colonize new habitats and expand their distributions (Lawler 2009; Lawson *et al.* 2012). Existing conservation programs could assist species' range shifts through a combination of statutory protection to prevent damage to habitats, and active conservation to enhance habitat quality and encourage colonization (Warren 1993; Nicholson *et al.* 2012). However, a key question is whether static networks of protected areas (PAs), established to safe-

guard ecological assemblages in situ, offer sufficient protection for range-shifting species, or whether more flexible, reactive approaches to conservation must be adopted (Gaston *et al.* 2006; Hannah *et al.* 2007; Thomas *et al.* 2012).

The evidence base for PA effectiveness under climate change comes largely from theoretical studies (Gaston *et al.* 2008; Thomas *et al.* 2012). Typically, range shift forecasts derived from species distribution models are coupled with maps of existing PA networks to assess which species will be protected under future climates (Hannah *et al.* 2007; Hole *et al.* 2009). These studies have generally predicted that climate change will drive species outside of their protected habitats, suggesting that failure to modify existing conservation measures will result in widespread biodiversity loss (Araújo *et al.* 2011; Coetzee *et al.* 2009; D'Amen *et al.* 2011; Hannah *et al.* 2007;

Zimbres *et al.* 2012; but see Hole *et al.* 2009). However, this conclusion rests on several assumptions. First, predictive approaches implicitly rely on accurate forecasts of species' range shifts, which cannot be verified without empirical data (Pearce & Ferrier 2000). Second, populations inside PAs are assumed to survive, but PA designation may be ineffective without management to maintain or improve habitat quality (Gaston *et al.* 2008; Nicholson *et al.* 2012). Third, populations outside of PAs are assumed to suffer extinction (Araújo *et al.* 2011), but the existence of potentially suitable habitat resources in unprotected parts of the landscape (Dennis 2012) could allow populations to persist outside of PAs, especially in the context of local adaptation (Merckx *et al.* 2003) and/or beneficial conservation management actions. There is thus a need for empirical research that assesses the extent to which (1) PA designation and (2) active conservation can facilitate range shifts.

Recent empirical work (Thomas *et al.* 2012) suggests that PAs are preferentially colonized during species' range expansions. However, this study did not dissect the relative roles of PAs and active conservation (Thomas *et al.* 2012). The increased colonization of PAs could thus reflect: (1) direct benefits of reduced habitat destruction; (2) indirect benefits, if PA designation encourages conservation interventions that maintain or improve habitat quality; and/or (3) that PAs act as a label for "high-quality" sites that would have been colonized anyway, in which case further legislation will be of limited effect. Examining the relative contributions of PAs and active conservation would help to explain *why* PAs are colonized more frequently than non-PAs, and assess the extent to which conservation actions outside of PAs can facilitate range expansions.

Here, we analyze the impacts of existing conservation approaches on the dynamics of an exemplar species, the silver-spotted skipper butterfly *Hesperia comma*, during a period of climate-driven range expansion. *H. comma* represents an excellent model system for this purpose, because it possesses traits shared by those species most vulnerable to global warming (Warren *et al.* 2001): it has highly specialized habitat requirements (Thomas *et al.* 1986); its range expansion has been hampered by the fragmented distribution of suitable habitats (Thomas *et al.* 2001; Lawson *et al.* 2012); and it has limited dispersal abilities (Davies *et al.* 2005). Using data collected across a network of 724 habitat patches across the British distribution of *H. comma*, we quantify the effects of PAs and conservation actions on the colonization and survival of *H. comma* populations at a 9-year interval. The results show that PAs facilitate range shifts both by preventing habitat destruction and by promoting conservation interventions that improve habitat quality, and that conservation inter-

ventions on nondesignated sites also have a role to play in adapting conservation to climate change.

Materials and methods

Our study takes place in Britain, where our study species, *H. comma*, reaches the northern margin of its geographic range. British populations of *H. comma* have highly specialized habitat requirements: eggs are laid exclusively on sheep's fescue grass *Festuca ovina*, generally on short tufts of the host plant <10 cm tall (Thomas *et al.* 1986), limiting populations to heavily grazed patches of unimproved calcareous grassland in which the host plant grows (Lawson *et al.* 2012). The distribution of habitats containing suitable *F. ovina* plants is patchy across the landscape: first because of the locations of chalk geology, second because of widespread agricultural improvement and abandonment, and third because of heterogeneous grazing pressure (Warren 1993). In Britain, thermal constraints on egg laying and activity restrict *H. comma* to sites with sufficiently warm ground surface temperatures (Davies *et al.* 2006). In other parts of its geographic range, *H. comma* remains specialized to a small number of host plant species (including *F. ovina*), but the specific preference for host plants growing in short turf may be weaker in warmer regions, where requirements for warm microclimates are likely to be reduced (Davies *et al.* 2006).

The distribution dynamics of *H. comma* in Britain over the past century reflect the importance of climate and habitat constraints on the presence of this species. In the early 20th century, *H. comma* populations were found in more northerly parts of Britain than at present, but a decline in traditional grazing regimes and the crash in rabbit population numbers caused by the introduction of the *Myxoma* virus resulted in a loss of suitable short-sward habitat, precipitating a range contraction to fewer than 70 populations by 1980 (Thomas *et al.* 1986). Since this time, the reintroduction of livestock grazing and recovery of rabbit populations has increased landscape-scale habitat availability, while rising summer temperatures have allowed *H. comma* to occupy cooler north-facing slopes, catalyzing a reexpansion (Thomas *et al.* 2001; Lawson *et al.* 2012).

We comprehensively surveyed the distribution of *H. comma* in Britain (encompassing the vast majority [*c.* 95%] of *H. comma* populations) in 2 years: 2000 and 2009. Habitat patches were defined as calcareous grassland with short (<10 cm) sward containing suitable *F. ovina* host plants. Patches were visited by field surveyors, who mapped the location and perimeters of each patch using handheld Global Positioning Systems (accuracy <±10 m); this information was later digitized to allow the calculation of patch areas (in hectares) and

their connectivity to other habitat patches. In each patch, in both 2000 and 2009, we used timed searches for adults and/or eggs to establish presence of *H. comma* (Lawson *et al.* 2012). We also collected information on the habitat attributes of each patch, including the proportional coverage of vegetation less than 10 cm in height, and the proportional coverage of the host plant *F. ovina* and bare ground (an important habitat resource for the butterfly because it provides warm microclimates for oviposition; Davies *et al.* 2006) within this short vegetation.

We classified each patch according to its protection status and its ongoing management. In the United Kingdom, protection of habitat against damaging activities is largely realized through designating Sites of Special Scientific Interest (SSSIs). SSSIs represent the basic level of site-based nature conservation legislation in the United Kingdom, and require the owners and occupiers of designated land to consult the official conservation body and obtain consent to carry out certain potentially damaging activities (Gaston *et al.* 2006). We classified patches that overlapped with SSSIs as *protected*, and those that did not as *unprotected*.

Short-sward grassland forms the home of several of Britain's most threatened butterflies, including the Adonis blue *Polyommatus bellargus* and the Large blue *Maculinea arion* (Thomas 1993; Thomas *et al.* 2009). Conservation management of chalk grassland in the United Kingdom is realized through maintaining livestock grazing at appropriate levels for chalk grassland biota, which increases local species richness by reducing competitive exclusion (Maalouf *et al.* 2012). We classified the management of habitat patches into three categories. Patches in which the primary purpose of the land was to promote biodiversity were classified as under *primary management*, which included land owned by Natural England (the official nature conservation body in England), local authorities, or nongoversnmental conservation organizations (e.g. the National Trust, County Wildlife Trusts). These primary managers conduct conservation actions aimed at promoting chalk grassland biodiversity in general, rather than species-specific management targeted toward *H. comma*. Patches managed by private landowners as part of voluntary "agri-environment schemes" (AES), in which payments are offered for management that benefits nature conservation, were classified as under *voluntary management*. Two such schemes, Environmentally Sensitive Areas (ESA) and the Countryside Stewardship Scheme (CSS), ran during the majority of the period of this study. We defined *unmanaged areas* as habitats that fell outside either of the two previous categories but which nevertheless fulfill the habitat requirements of our focal species (chalk grassland containing Sheep's fescue grass *F. ovina* growing in short turf). We derived

Table 1 Management groupings used in statistical models

| Variable name	Management category		
	Primary	Voluntary	Unmanaged
Primary	1	2	2
Voluntary	2	1	2
Unmanaged	2	2	1
Management	1	2	3

Factors with different codings were generated, comprising either: two levels, in which one management category was distinguished from the others (*primary*, *voluntary*, or *unmanaged* groupings); or three levels, one for each management type (the *management* grouping).

SSSI, CSS, and ESA status using the *rgeos* library in *R* (R Development Core Team 2011; Bivand & Rundel 2012) and shapefiles available from Natural England (2012).

We tested the effects of management on: (1) colonization, by 2009, of patches that were not occupied by *H. comma* in 2000 and (2) population survival, in 2009, of patches that were occupied in 2000. Colonization and survival probabilities were modeled using generalized linear models in *R* (R Development Core Team 2011), assuming a Bernoulli error structure. To assess the effects of PAs and conservation interventions while controlling for other determinants of colonization and survival, we used the top-fitting models from a previous analysis (Lawson *et al.* 2012) as null models, to which terms were subsequently added (the previous analysis included patch area, connectivity, vegetation characteristics, and climate variables; see Appendix S1). *Protection* was modeled as a factor with two levels: *protected* and *unprotected*. *Management* was modeled as a factor with up to three levels (Table 1). Models were competed based on the corrected version of Akaike's information criterion (AICc; Richards 2008) using the *AICcmodavg R* package (Mazerolle 2012), and excluding models that had higher AICc scores (indicating a less parsimonious fit to the data) than their simpler nested variants (Richards 2008). To examine the extent to which our findings could be explained by spatial autocorrelation effects, we also fitted mixed models of colonization and survival that included spatially autocorrelated model terms; however, accounting for spatial autocorrelation did not substantially alter the important conclusions, so we only report these analyses in Appendix S2.

Results

Of the 510 habitat patches that were unoccupied by *H. comma* in 2000, 105 were colonized between 2000 and 2009. Of the 214 *H. comma* preexisting populations
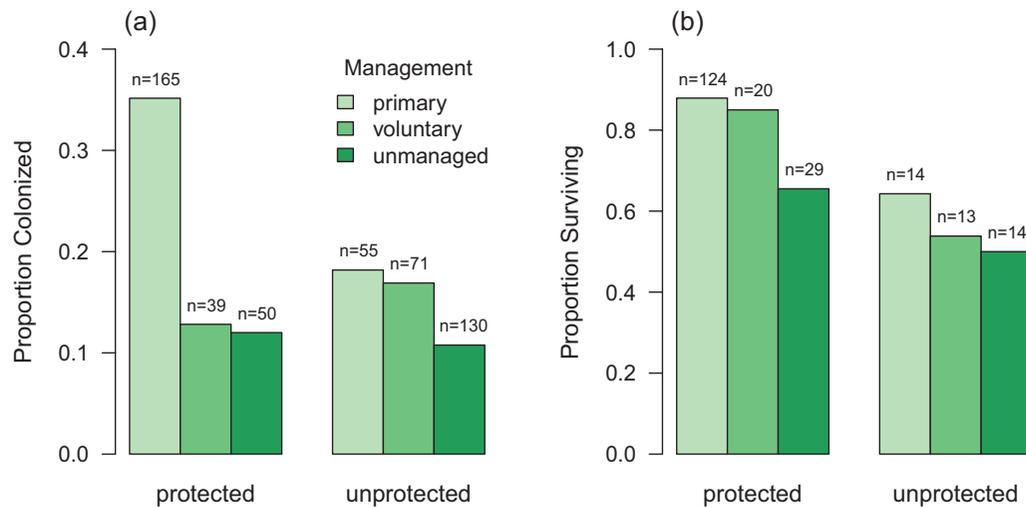
Figure 1 Effects of protection status and management on (a) the proportion of empty patches that were colonized and (b) the proportion of populations to survive between 2000 and 2009. Bars indicate raw proportions unadjusted for other habitat patch attributes. The "*n*" indicates the sample size for each category; note that sample sizes refer to the total number of populations or habitat patches studied (survival: 214 populations that were present in 2000; colonization: 510 habitat patches that were unoccupied in 2000).

recorded in 2000, 168 remained in 2009 (46 habitat patches no longer held populations, despite generally suitable habitats remaining). Across all sites, habitat patches in PAs were more likely to be part of primary conservation schemes than patches outside of PAs (Figure 1; chi-squared test of association: $\chi^2_2 = 139.6$, $P < 0.00001$), suggesting that PA designation encouraged active conservation management. Figure 2 displays changes to the distribution of *H. comma* between 2000 and 2009 in map form, with sites that were in protected areas and under primary management shown in red.

Patches under primary management were more likely to be colonized than voluntarily managed or unmanaged sites (Figure 1a; all top-ranked colonization models included a positive effect of primary management, Table 2). Moreover, protection status interacted with primary management, such that primary management produced a greater increase in colonization probability in PAs than in unprotected sites (*primary * protection* model ranks 5.8 AICc units below next best model, indicating a more parsimonious fit to the data; see Table 2). Overall, PAs under primary management were over three times more likely to be colonized than unmanaged, unprotected sites (Table 2; Figure 1a).

The best colonization models did not distinguish between voluntary and unmanaged sites (Table 2), even though the raw data indicate that a higher proportion of sites in voluntary management were colonized (Figure 1a). Examination of habitat variables (Appendix S4) showed that voluntarily managed sites tended to

be situated in higher-connectivity landscapes compared to unmanaged sites, suggesting that the more frequent colonization of voluntarily managed sites can be explained by their location rather than direct benefits of management.

We found reasonable evidence that primary management improved the survival of *H. comma* populations (Figure 1b; *primary + protection* model ranks 2.3 AICc units below *protection* model, and *primary* model ranks 5.1 units below *null* model, Table 2). However, there was considerable uncertainty as to whether AES improved population survival: the raw data indicated that population survival was more likely on voluntarily managed sites than unmanaged sites (Figure 1b), but this difference was not statistically meaningful once other determinants of patch occupancy were controlled for (Table 2). As in the colonization analyses, the higher survival of populations in voluntarily managed sites (Figure 1b) could be explained by their location and habitat attributes, rather than management effects: sites under voluntary management were larger than unmanaged sites, and tended to be found in better-connected habitat networks (Appendix S4).

Our analyses revealed that there exists substantial uncertainty as to whether statutory protection improved the survival of *H. comma* populations. The higher survival of populations in PAs than in non-PAs (Figure 1b) appears to be a byproduct of landscape context and climate: sites that were situated in better-connected habitat networks and in warmer regions of Britain (with higher mean
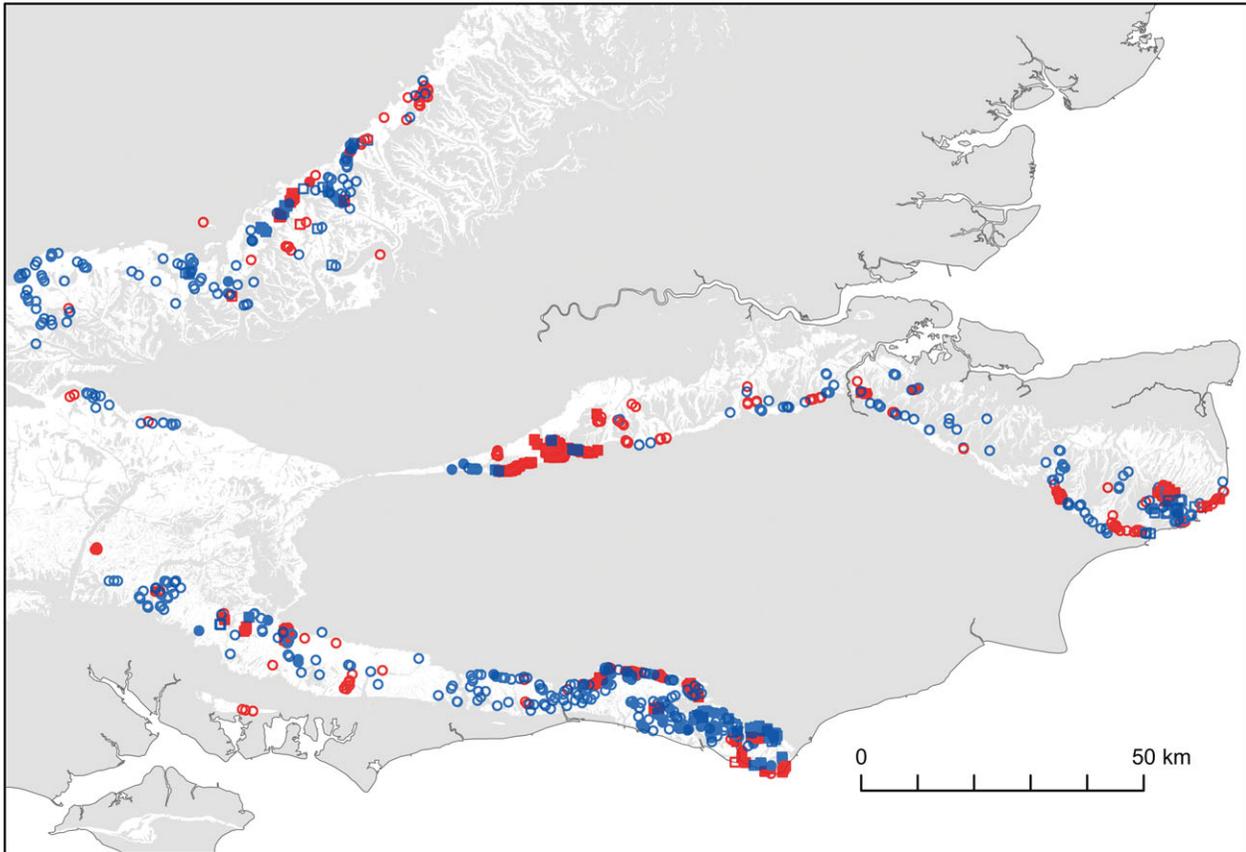
Figure 2 Map illustrating the importance of protection status and primary conservation management on the distribution dynamics of *H. comma* in Britain between 2000 and 2009. Each symbol represents an individual habitat patch; symbol shape indicates whether the patch was occupied (squares) or unoccupied (circles) in 2000, while symbol fill indicates whether the patch was occupied (filled) or unoccupied (empty) by 2009. Patches that are situated in protected areas and are under primary management are shown in red; all other patches are shown in blue.

August maximum temperatures) were more likely to receive protected status (Table 2; Appendix S4). Furthermore, populations surviving in PAs tended to be spatially clustered (Figure 2), such that the apparent benefit of PAs on population survival may have been exaggerated by spatial autocorrelation effects (Appendix S2).

Discussion

Our analysis of the metapopulation dynamics of *H. comma* provides empirical evidence that preexisting conservation measures can provide effective means to facilitate range expansions, even when not specifically established to deal with climate change impacts. The results show that PA designation greatly increased colonization rates of unoccupied habitat, despite being designed to protect species over preexisting, implicitly static distributions (Gaston *et al*. 2006; Thomas *et al*. 2012). By

examining the range expansion of *H. comma* at the level of individual populations, we also demonstrated *why* PAs increased colonization chances: first, because PAs directly protected key habitat patches from destruction, and second, because their designation encouraged active conservation actions (in our system, realized through management, e.g. appropriate grazing levels; Warren 1993; Maalouf *et al*. 2012) that promoted habitat quality (Figures 1 and 2). Thus, our findings encourage the idea that existing PAs can continue to form an important component of biodiversity conservation under climate change.

The ability of PAs to protect biodiversity may be critically dependent on how they are managed (Gaston *et al*. 2008; Nicholson *et al*. 2012). In our study, conservation interventions were integral to the success with which PAs facilitated the range expansion of *H. comma*; the combination of statutory protection and active

Table 2 Top-ranking models for colonization (a) and population survival (b) in *H. comma* habitat patches

| | | | | Predicted colonization or survival probability (%) | | | | | |
| | | | | Protected | | | Unprotected | | |
Variables in model	K	δAICc	LL	Primary	Voluntary	Unmanaged	Primary	Voluntary	Unmanaged
(a) Colonization									
Primary * protection	7	0.0	− 172.2	28.2	5.1	5.1	9.3	8.3	8.3
Primary	5	5.8	− 177.2	23.2	7.5	7.5	23.2	7.5	7.5
(b) Survival									
Primary + protection	9	0.0	− 78.7	91.7	81.8	81.8	83.2	67.0	67.0
Primary	8	0.6	− 80.1	90.7	77.2	77.2	90.7	77.2	77.2
Protection	8	2.3	− 80.9	88.7	88.7	88.7	73.7	73.7	73.7
Voluntary	8	4.7	− 82.1	88.2	75.9	88.2	88.2	75.9	88.2
Unmanaged	8	4.8	− 82.2	87.8	87.8	78.1	87.8	87.8	78.1
Null	7	5.1	− 83.4	86.1	86.1	86.1	86.1	86.1	86.1

K = number of parameters; δAICc = difference in AICc between model and top model; LL = log-likelihood. Only models with δAICc ≤6 are shown. The (*) symbol indicates a statistical interaction. Note that all models, including the "null" model, include patch attributes found to be statistically important in a previous study (Appendix S1). The six right-hand columns show predicted probabilities of colonization (a) or survival (b) for a habitat patch with average attributes (Appendix S3).

conservation generated a three-fold increase in colonization rates, but the benefits of protection and primary conservation were diminished when employed in isolation (Figure 1a). This finding emphasizes that PA designation may be of limited benefit for range-shifting species without conservation interventions to maintain or improve habitat quality. Moreover, our analysis of the survival of *H. comma* populations indicates that active conservation interventions can help to preserve vulnerable range-edge populations outside of PAs, consolidating gains made during periods of expansion (Figure 1b). Appropriate habitat management activities both inside and outside of reserves is thus likely to be key to efficient range shift management.

Due to constraints on the resources available for data collection, empirical assessment of the conservation value of protected areas often relies on either indirect evidence from national scales (Van Dyck *et al.* 2009), or direct evidence from more localized scales. By analyzing the establishment and survival of populations in individual habitat patches, we were able to assess the benefits of PA designation directly at a national scale, encompassing virtually all *H. comma* populations in Britain and lending a level of control not achievable in previous assessments of PA effectiveness under climate change (Araújo *et al.* 2011; Thomas *et al.* 2012). We only studied potentially suitable *H. comma* habitats of the same vegetation and geology type, such that our analyses did not represent unfair comparisons between PAs and elements of the wider landscape that could not have been colonized. More-

over, the impacts of conservation actions could be quantified while controlling for the effects of other environmental variables influencing habitat patch occupancy, which allows two strong conclusions. First, PAs and "primary" management (where conservation is the primary aim) have positive effects over and above the habitat quality attributes influencing site designation. Second, voluntary agri-environmental conservation schemes have at best weak effects on the range expansion rates of *H. comma*; raw colonization and population survival rates suggest apparent benefits of voluntary management (Figure 1), but detailed examination shows that these benefits are likely to be a byproduct of the high quality and connectivity of sites selected for management (Table 2; Appendix S4). We therefore remain cautious about the success with which voluntary AES facilitate range shifts.

Modeling studies have predicted that climate change will force many species to shift their distributions outside of PA networks (Coetzee *et al.* 2009; Araújo *et al.* 2011; D'Amen *et al.* 2011; Zimbres *et al.* 2012), suggesting a need to adopt more dynamic designation approaches (Hannah *et al.* 2007). Methods to plan PA networks that will enable range shifting have been proposed (Phillips *et al.* 2008; Hodgson *et al.* 2011), and are likely to be needed to some extent to conserve biodiversity under climate change. For example, the continued expansion of *H. comma* in the United Kingdom is contingent on the availability of suitable habitats to colonize, but the rapid expansion of this butterfly has meant that populations have

started to "fill up" available habitat networks, with fewer unoccupied patches within the dispersal distance of adult butterflies (particularly in Surrey, the central habitat network depicted in Figure 2). Efficient management of the range shifts of this and other species is thus likely to involve a blend of preexisting conservation management to improve the suitability of current habitats, and new approaches to encourage the provision of new habitats to colonize. Nonetheless, these new approaches have yet to be tested empirically, and changing ownership or legal status, changing habitat (e.g. restoring from agricultural land), and changing management regimes all have associated costs and uncertainties, so it is vital to have empirical indications of what can be achieved with existing measures.

For *H. comma*, we have shown that existing conservation management plans can facilitate species' range expansions through established PA networks, and protect newly established populations both inside and outside of these networks. These findings are particularly encouraging because the primary conservation actions investigated here reflect a range of generic approaches in addition to more directed management for *H. comma*. This means that: (1) the benefits of the system-specific management actions (e.g. grazing to maintain short sward) are likely to be shared by many other grassland species with similar habitat preferences, including other threatened butterflies such as the Adonis blue *Polyommatus bellargus* and Large blue *Maculinea arion* (Thomas 1993; Thomas *et al.* 2009), but also that (2) broad-brush conservation interventions to maintain high habitat quality can assist species' range shifts even when not specifically tailored toward a particular species. Our findings are also likely to transfer to other systems that share those traits that identify *H. comma* as at risk from climate change: namely, species with highly specialized habitat requirements, fragmented habitat networks, and/or limited dispersal abilities (Warren *et al.* 2001). As such, the results of this study suggest that current conservation measures will be an integral and cost-efficient part of multispecies strategies to preserve biodiversity under climate change.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1: Null model structures.
Appendix S2: Investigating the influence of spatial autocorrelation.
Appendix S3: Detail on method for predicting colonization and survival probabilities.
Appendix S4: Relationships between management categories and variables in null models.
This material is available as part of the online article from:

http://www.blackwell-synergy.com/doi/full/10.1111/ j.1755-263X.2008.00002.x
(This link will take you to the article abstract).

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