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LETTER

High Abundances of Species in Protected Areas in Parts of their Geographic Distributions Colonized during a Recent Period of Climatic Change

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Abstract

It is uncertain whether Protected Areas (PAs) will conserve high abundances of species as their distributions and abundances shift in response to climate change. We analyzed large datasets for 57 butterfly and 42 odonate species (including four that have recently colonized Britain). We found that 73 of 94 species with sufficient data for analysis were more abundant inside than outside PAs in the historical parts of their British distributions, showing that PAs have retained high conservation value. A significant majority (61 of 99 species) was also more abundant inside PAs in regions they have colonized during the last 30–40 years of climate warming. Species with relatively high abundances inside PAs in long-established parts of their distributions were also disproportionately associated with PAs in recently colonized regions, revealing a set of relatively PA-reliant species. Pas, therefore, play a vital role in the conservation of biodiversity as species' ranges become more dynamic.

Introduction

Protected Areas (PAs) are a cornerstone of global, national, and local conservation policies (Chape *et al.* 2005; Jackson & Gaston 2008; Convention on Biological Diversity 2010; Soutullo 2010; Harrop 2011), but their capacity to retain their biodiversity value in the context of rapid environmental change is uncertain. There is already strong evidence that local abundances and habitat associations are changing (Suggitt *et al.* 2012), and that species are shifting their geographic ranges polewards and to higher elevations as a result of rising temperatures (e.g., Warren 1999; Hickling *et al.* 2006; Parmesan *et al.* 1999; Chen *et al.* 2011). This provides challenges for biodiversity conservation. Climate change could result in (1) altered patterns of abundance, such that PAs may no longer hold the highest abundances of a given species, (2) the loss of species from some of the PAs that they currently occupy and (3) colonization of new regions, where they may or may not colonize already-established PAs (e.g. Araújo *et al.* 2004, 2011; Coetzee *et al.* 2009; D'Amen *et al.* 2011; Thomas *et al.* 2012). Overall population trends (which determine red listing and eventually survival) will depend on the balance between losses in species' historical ranges and gains within newly colonized areas. Similarly, the level of conservation provision by PAs will depend on the balance between population losses in PAs within historical distributions and population gains in PAs within newly colonized areas.

Here, we evaluate whether PAs facilitate population gains by supporting large populations of species as they expand polewards into new regions. Availability of thermally suitable habitats toward the edge of species' ranges (Thomas *et al.* 1999) and habitat fragmentation (Hill *et al.* 2001) may limit or prevent the expansion of some species. Despite this, expanding species are already colonizing PAs (Thomas *et al.* 2012; Hiley *et al.* 2013), and hence, PAs may be effective at conserving species in new parts of their range. This argument would be strengthened if PAs support large populations of associated species in regions that have recently been colonized. Whilst this may seem intuitive, little work has been done to quantify the differences in abundance of species within and outside PAs, even within species historical, or core, ranges (Hodgson *et al.* 2010), and virtually nothing is known of abundances inside and outside of PAs in newly colonized parts of species' distributions.

We use national records from Britain for two invertebrate groups, one terrestrial and the other primarily freshwater, to identify whether greater abundances of species exist within PAs than are found outside PA boundaries. Butterflies and odonates were the taxa of choice primarily because British naturalists have been recording these insects extensively over the last 50 years (Asher *et al.* 2001; Parr 2010). As a result, data are available not only for the distributions of these species, but also often for their abundances at the time and place of recording. In addition, these groups have shown marked distribution changes in response to climate change (Parmesan *et al.* 1999; Hickling *et al.* 2005, 2006).

There are three main aims to this study. First, we assess the abundances of butterflies and odonates where they have been recorded inside and outside PAs across their entire British ranges, and also within the subset of locations where they have occurred for longest (i.e., their "historical" or "core" ranges). This provides an indication of the relative qualities of habitats for these species inside and outside PAs, and enables us to assess whether British PAs have high conservation value, 30–40 years after the onset of rapid regional warming in the 1970s. Second, we evaluate whether populations of species that have recently colonized new areas were greater inside PAs than outside them in their recently colonized ranges. This would indicate the importance of existing PAs in supporting the establishment of species as they colonize new regions. Third, we evaluate whether PA-reliant species within their historical ranges are also disproportionately abundant within PAs in the regions of recent colonization. The answers to our second and third questions also provide insight into the ability of PAs to protect biodiversity more broadly because reserves outside the previous distributions of species were not selected with these species in mind, hence high numbers of colonists in these locations would indicate high quality habitats.

Table 1 Standard abundance categories used by the dragonfly recorders network and the butterflies for the new millennium recording scheme. Shown here is the number of individuals (*N*) in each category for each scheme, and the ordinal category allocated to each in this study

Category	*N* (odonates)	*N* (butterflies)	Ordinal category
A	1	1	1
B	2–5	2–9	2
C	6–20	10–29	3
D	21–100	30–99	4
E	101–500	100+	5
F	>500	NA	6

Methods

Using data from the Dragonfly Recording Network and the Butterflies for the New Millennium recording scheme, we considered all butterflies and odonates with confirmed breeding within Britain. We defined core (long established) and colonized (recently established) ranges for each species. The core range was defined as all those national Ordnance Survey 10 × 10 km grid squares where a target species had been recorded during time period T_1, as defined by Hickling *et al.* (2006) because of the availability of suitable baseline data for these periods; that is, 1960–1970 for odonates, 1970–1982 for butterflies. The colonized range of a species was defined as all those 10 × 10 km grid squares where the target species was recorded as absent in T_1 (i.e., the square was recorded as having other species in the same taxonomic group present in T_1, but the target species was not recorded as present) but present in the second recording period, T_2 (1985–2010 for odonates, 1995–2010 for butterflies). It should be noted that many species that are colonizing new areas are undergoing declines in other parts of their ranges within the UK (Asher *et al.* 2001, Fox *et al.* 2006), so expansion into newly colonized parts of the range does not necessarily imply that their overall range size has increased.

For analysis of associations with PAs, we considered only those records at 100 × 100 m resolution or finer; and we restrict the analysis of PA-associations to T_2, when the majority (>65%) of records were at this resolution. We then filtered the data to include only records where abundance information was available. Abundances were typically recorded using the categories recommended by the respective recording schemes (see Table 1) but in some cases the number of individuals was recorded directly. We removed records where cumulative totals had been recorded over the course of a year, so that abundances reflect numbers observed at a given time and location. We formatted all records to the ordinal categories in

Table 1. All finer resolution records were harmonized to 100×100 m resolution.

We defined PAs, after discussion with a stakeholder group (see acknowledgements), as Sites of Special Scientific Interest (SSSIs), representing IUCN category IV protection, which aims to protect a set of target species or habitats (IUCN 1994). Locations of SSSI boundaries were obtained from Natural England, Scottish Natural Heritage and the Countryside Council for Wales. Because adults of both taxa disperse and forage using flight, we categorized the abundance records as associated with a PA if any of the 100×100 m square representing the recorded location lay within a PA boundary (using ArcMap v. 10, ESRI, Redlands, CA, USA). We used Mann-Whitney U tests to compare the median abundance category within species as follows:

(1) Inside and outside PAs across the entire range for all 95 species historically resident in Great Britain.
(2) Inside and outside PAs in the core range of the 94 species with sufficient data for this analysis.
(3) Inside and outside PAs in the colonized range of all 95 historically resident species plus four recent colonists with confirmed breeding in Great Britain.
(4) Between the core and colonized ranges of the 95 historically resident species.

Due to multiple tests being carried out, Bonferroni corrections were applied by dividing the normal threshold P value of 0.05 by the number of tests (383). Outcomes are only reported as significant if the P value is less than this revised threshold.

We also used Wilcoxon Signed-Rank tests to compare abundances inside/outside PAs and also between the core and colonized range across all species for the above four categories. Spearman's Rank correlation was used to compare the benefit conferred by a PA (i.e., abundance inside PAs/abundance outside PAs) between the core and colonized ranges of species. For this analysis, we removed any species with fewer than 30 records in either the core or colonized part of its range and fewer than 10 records in PAs or outside PAs (i.e., the ratio of PA use could not be reliably calculated). All statistical analyses were carried out in R version 2.13 (R Core Team 2012).

The data were collected by volunteers. Such recording is largely undirected, so there could be a number of biases related to the likelihood that sites will receive visits and the durations of those visits (Dennis & Thomas 2000). This is why we only compare abundances in locations where a given species has been recorded as present at 100 m grid resolution, indicating that the site has been visited at least once during the species' period of activity and under conditions sufficient to record the species. Most biological recorders who are completing the abundance field of a recording form at 100 m resolution are likely to report everything seen. It is also why we exclude cumulative records (above). If more than one abundance record was available for a single location, we used the mean of the abundance categories of all the records to ensure that locations that were visited multiple times were not counted more than once. It is still possible that a naturalist might spend more effort (duration) under suitable conditions recording during a visit to a PA than elsewhere, potentially thereby recording a higher abundance category. However, several species were recorded as significantly more abundant outside rather than inside PAs (see results), so recording behavior does not inevitably result in higher abundances being recorded inside PAs. In addition, a pilot study with equal recording effort in and outside PAs (see supplementary materials S1) indicated that odonate abundance is higher on ponds inside PAs than on similar ponds located outside PAs.

Results

Across the 95 historically resident species, 76 (80%) species were more abundant in PAs than outside across their entire ranges (Figure 1a, Wilcoxon Signed-rank test, $N = 95$, $V = 3844$, $P < 0.0001$). Individually, 42 species (44%) occurred at significantly higher abundance in PAs than outside, whilst one showed the opposite pattern (see supplementary tables S2 and S3).

Of the 94 species with sufficient data, 73 (78%) were more abundant inside than outside PAs within their core range (Figure 1b, Wilcoxon signed-rank test, $N = 94$, $V = 3615.5$, $P < 0.0001$), whilst 61 of all 99 species (62%) were more abundant inside than outside PAs in their colonized range (Figure 1c, Wilcoxon Signed-rank test, $N = 99$, $V = 3325.5$, $P = 0.0015$). When examined individually, 38 (40%) species were significantly more abundant in PAs within their core range (one showed the opposite pattern) and 12 (12%) species were significantly more abundant in PAs in their colonized range (one was significantly more abundant outside PAs, see supplementary tables S4–S7).

Seventy-nine of the 95 historically resident species were more abundant in their core range than their colonized range (Figure 1d, Wilcoxon Signed-rank test, $N = 95$, $V = 4073$, $P < 0.0001$). Individually, 30 (32%) were significantly more abundant in their core ranges, with two being significantly more abundant in colonized locations (see supplementary tables S8 and S9).

The relative abundance of species inside and outside PAs was correlated between the long established (core) and recently colonized parts of species ranges (Figure 2, Spearman's Rank Correlation, rho = 0.41, $P = 0.0001$,

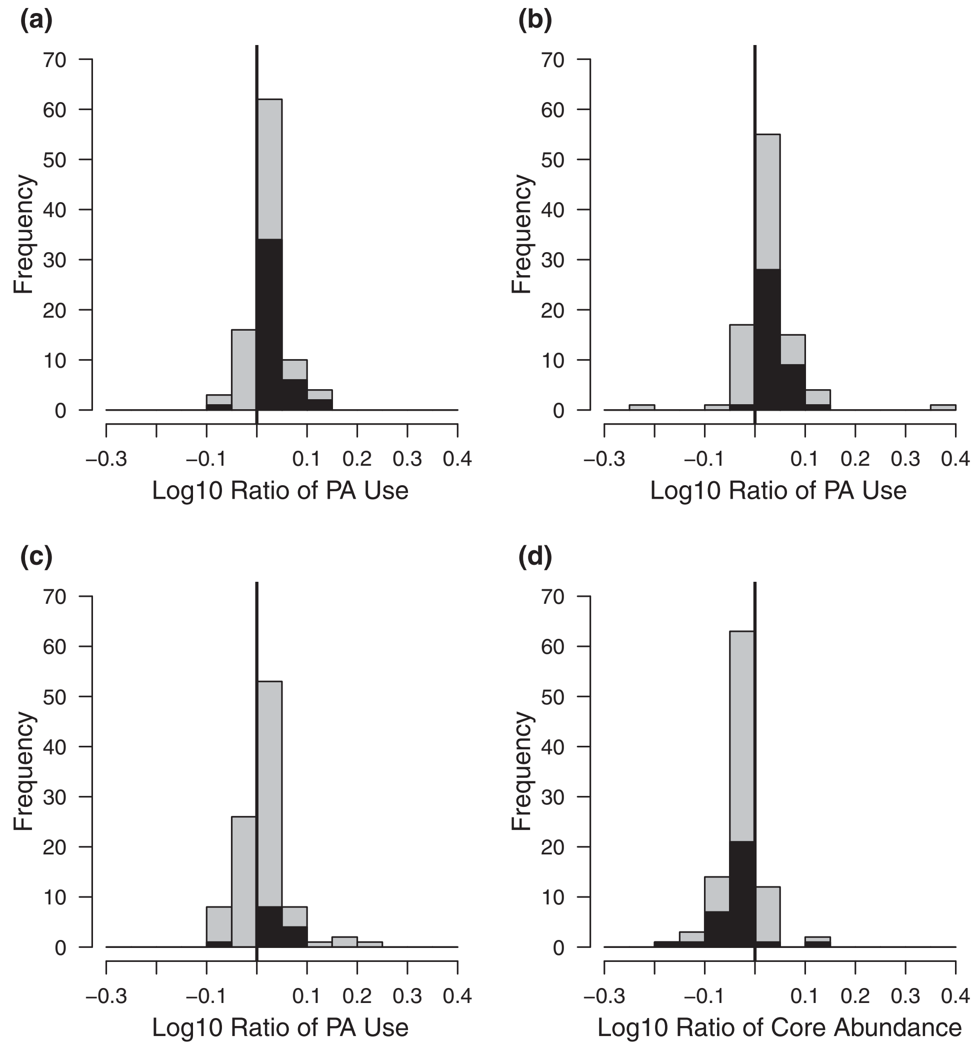

Figure 1 Histograms showing frequencies (numbers of species) with ratios between (a) Abundance on PAs compared to non-PAs for the entire range of all species; (b) Abundance on PAs compared to non-PAs in species' core ranges; (c) Abundance on PAs compared to non-PAs in species' colonized ranges; (d) Abundance in core range compared to colonized range. For (a)–(c), a log ratio >0 means that the species is more abundant on PAs. In (d), a log ratio <0 means that the species is more abundant in its core range. Grey bars represent all species, black bars represent those species that are individually significant after the application of Bonferroni corrections.

$N = 84$). Hence, species that rely most on PAs in their historical range also tend to rely most on PAs in their new ranges.

Discussion

pc With a few exceptions, abundances were higher within, versus outside, PAs. This is the case even in newly established parts of species' ranges, indicating that the conditions present in PAs are generally favorable to the establishment of substantial populations, facilitating range expansion. Effect sizes were small in many cases (see supplementary tables S2–S9), but because abundance categories represent larger absolute numbers of individuals, even small differences in abundance category could potentially translate to large differences in numbers of individuals. It is worth noting that the existence of a few species with significantly lower abundance outside nature reserves than inside them (Figures 1a–c) indicates that recording by naturalists (see methods) does not inevitably result in higher abundances being recorded within PAs.

In addition, species that were found in larger numbers on PAs in their core range tended to be found in larger numbers on PAs in their colonized range as well.

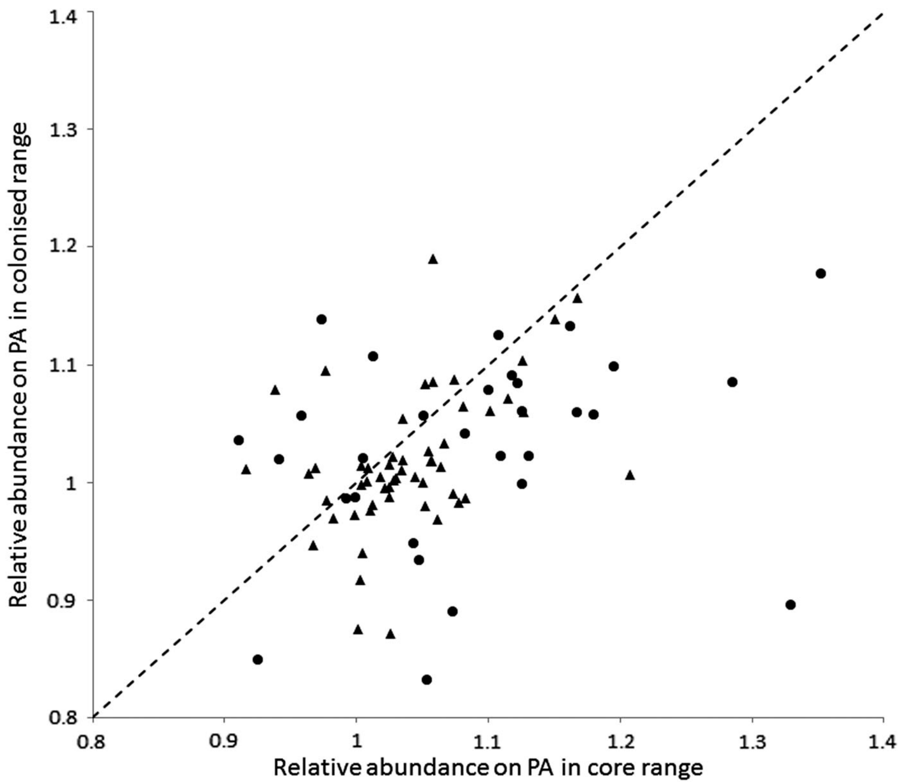

Figure 2 The relationship between the bias toward protected areas (PAs) in core (historical) range and newly colonized range. Butterflies are indicated by filled triangles, odonates by filled circles. The dashed line represents the 1:1 line, where association toward PAs is equal in core and colonized parts of the range.

Therefore, species that most rely on PAs in their established range also benefit from PAs in their colonized ranges, where they were not explicitly designated with these species in mind. However, the relationship we observed is relatively weak, indicating that other, unmeasured factors also affect the abundance of species across their ranges.

Several characteristics of SSSIs might explain why they contain increased abundances of butterflies and odonates. In the core parts of species' ranges, the process of SSSI designation may go part way to explaining the relatively high abundances of species within them. SSSI designation is directed toward large, natural environments that already exhibit high biodiversity (NCC 1989). Butterflies and odonates are considered directly as a component of animal species diversity during SSSI allocation and there is an emphasis on population size during the allocation process (NCC 1989, JNCC 1998). Hence, sites containing large populations of these groups may have been selected disproportionately. Nonetheless, large populations will only have remained large since designation if habitat conditions continued to be favorable.

The legal protection conferred by SSSI status specifies that certain damaging activities may not be carried out without consent (Natural England 2011) and SSSIs have subsequently been managed to increase habitat quality: management aims to maximize the fraction of SSSI land defined as "in favorable condition" for wildlife, and to adopt management such that previously unfavorable sites achieve "recovering" or "favorable" status (DEFRA 2011). Pollution is also alleviated by legal protection in both terrestrial and inland aquatic environments (Biggs *et al.* 2005). This prevention of harmful activities and management to increase numbers of target species would be likely to maintain populations within SSSIs in their core ranges, whilst populations outside them might deteriorate (but see Davies *et al.* 2007).

In addition, SSSIs represent the only locations with enough suitable habitat to support breeding populations of some species. In England, a number of butterfly habitat specialists (e.g., *Hesperia comma*, *Polyommatus bellargus*, *P. coridon*, and *Melanargia galathea*) are associated with lowland calcareous grasslands, for which 69.8% of the total area falls with SSSIs, and inland populations of *Plebejus argus* and *Hipparchia semele* are largely restricted to lowland heathland, with 73.9% of the area within SSSIs (percentages of habitat areas in SSSIs from Lawton *et al.* 2010). However, there is no one-on-one correspondence between the land use and habitat categories that have been defined for the purposes of conservation designation, as summarized in Lawton et al. (2010), and the requirements of individual species. The aforementioned *P. argus*, for example, uses only a subset of inland heathland habitat types (where mutualistic *Lasius* ants occur at sufficient densities, Jordano *et al.* 1992), and yet the butterfly uses additional habitats along the coasts (a subset of dunes and calcareous grasslands, where *Lasius* ant densities are also high, Jordano & Thomas 1992). Hence, it is not possible to enumerate exactly what percentage of a given species' potential habitats is confined to SSSIs from remotely sensed or vegetation community data. The situation is even more complex in the odonata, for which habitat associations tend to be determined by the flow rates and chemical properties of water rather than the presence of specific habitat categories, as defined by humans (Smallshire & Swash 2010). An exception is *Orthetrum coerulescens*, which is characteristic of wet heath in Britain, the majority of which is found in SSSIs (71.7% of upland heath and 73.9% of lowland heath, although these figures include both wet and dry heath, Lawton *et al.* 2010). Thus, most of the large populations of habitat specialists tend to be confined to SSSIs because the same types of habitat are largely destroyed or degraded elsewhere. However, there are exceptions, as in case of the specialist dragonfly *Aeshna isosceles*, which in England is largely restricted to ditches on grazing marsh, of which only 17.5% falls within PAs (Lawton *et al.* 2010).

Avoidance of harm and management to improve habitat quality and quantity will also affect the abundances of species in newly colonized regions. Species' prior abundances, by contrast, could not have been a factor because the species were not present in these regions at the time of site designation. This may partly explain why fewer species are significantly associated with SSSIs in their colonized ranges. However, we suggest that the apparently slightly weaker benefit of PAs in colonized regions is more likely to result from (1) generally smaller colonized ranges than core ranges (small sample size of sites per species), leading to greater uncertainty of effect sizes and lower statistical power for detecting effects, (2) lower overall abundances and greater population size variability in new parts of species' ranges (Figure 1d, Thomas *et al.* 1999), leading to reduced contrasts in abundances (given that this analysis does not include absences) between locations inside and outside PAs, and (3) the somewhat poorer habitat condition of upland than lowland SSSIs (Kirby *et al.* 2010), given that species have expanded poleward and uphill in response to climate change (Hickling *et al.* 2006), so more such sites may be included within the colonized ranges.

Abundance of the Banded Demoiselle *Calopteryx splendens* was significantly lower inside PAs. This species reproduces in slow flowing streams, rivers, and canals (Smallshire & Swash 2010). Just 28% of SSSIs with streams and rivers and 35% with canals are considered to be in favorable or recovering condition and only 6% of streams and rivers, and 2% of canals are represented inside SSSIs in England (Natural England 2008). This may partly explain the low abundance of this species inside SSSIs.

One butterfly species, the White-letter Hairstreak *Satyrium w-album*, was significantly more abundant outside PAs in the core part of its range. This could have arisen because its elm *Ulmus* host plant was predominantly used in hedging and as hedgerow trees in lowland England in otherwise relatively intensively farmed areas. Following the arrival of Dutch elm disease in the late 1960s, almost all mature elms died, leaving low-growing plants in hedgerows in farmland and mature trees in a few urban areas (Asher *et al*. 2001), neither of which are likely to have been designated as SSSIs (Lawton *et al.* 2010).

Many species show higher abundances in their core than colonized range (Figure 1d). These differences in abundance may have constrained our ability to detect differences in abundance between PAs and non-PA land in newly colonized areas. Reduced densities are likely to arise from the time taken for populations to grow from their original establishment in recently colonized sites (Willis *et al*. 2009), even if climatic and other habitat conditions are equally suitable in core and colonized regions. In addition, climatic conditions do vary between core and colonized ranges, and populations of poikilotherms such as the species investigated here are often sparse and specialized toward the cool edges of their ranges (Thomas *et al.* 1999). Many of the colonized ranges considered here occur at cooler latitudes than the core ranges (Hickling *et al.* 2006), and cool conditions tend to result in reduced survival and population densities of the taxa considered (Corbet 1999; Roy *et al*. 2001).

From the evidence presented here, it appears that PAs do indeed contribute to nature conservation by providing suitable, high quality habitats that support larger populations than are found outside PAs. This is true both across species' entire ranges, and in locations that have recently been colonized. Despite concerns about some species moving out of PAs (Araújo 2004; 2011), other species of conservation concern colonize PAs (Thomas *et al.* 2012, Hiley *et al.* 2013) so the justification for safeguarding these habitats as climate changes remains robust. Reserve managers in the UK already monitor and manage habitats for some species that they were not designated for (Davies *et al.* 2007). We suggest that this practice of monitoring and management for colonizing species is sensible in the light of our results, and that any future classification of PAs as in favorable condition or otherwise (e.g. DEFRA 2011) should include consideration of colonizing species in addition to those species and habitats that the PA was designated for. Any degazettement of PAs (e.g. Fuller *et al.* 2010, Mascia & Pailler 2011) should not occur until colonizing species of conservation concern have been included in the assessment of PA performance.

Increasing the coverage of PAs (Lawton *et al.* 2010, Harrop 2011), preserving high quality habitats in regions that species are likely to colonize (Hannah *et al.* 2007) and recreating habitats (Lawton *et al.* 2010) remain valid approaches to the conservation of biodiversity under climatic change.

Acknowledgments

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Supporting Information

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

Supplementary materials 1 Details of a Pilot Study on Odonate abundance inside and outside PAs.

Figure S1. Map of the study area, showing the relative location of the four SSSIs (green fill) and the pairs of ponds within them (blue fill): (a) Strensall Common, (b) Askham Bog, (c) Skipwith Common, (d) Derwent Valley.

Figure S2. Odonate abundance (number of individuals observed in 10 minute sample periods) recorded inside and outside SSSIs at six pairs of ponds. Inside indicates the pond sampled in the SSSI, outside indicates the paired pond sampled on the same day outside the SSSI.

Table S2: Results of the Mann-Whitney U tests to compare the median abundance category of records inside PAs with the median abundance category of records outside PAs across species entire ranges for the butterflies. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located outside PAs (nonPA) and inside PAs (PA); The mean abundance category for all records outside PAs (MeanNonPA) and inside PAs (MeanPA); the test statistic (W); the calculated effect size (effect, note that a negative effect size means the species is more abundant inside PAs than outside); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, * denotes abundance category in PA is significantly higher than category outside PA, † denotes abundance category in PA is significantly lower than category outside PA after the application of Bonferonni corrections).

Table S3: Results of the Mann-Whitney U tests to compare the median abundance category of records inside PAs with the median abundance category of records outside PAs across species entire ranges for odonates. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located outside PAs (nonPA) and inside PAs (PA); The mean abundance category for all records outside PAs (MeanNonPA) and inside PAs (MeanPA); the test statistic (W); the calculated effect size (effect, note that a negative effect size means the species is more abundant inside PAs than outside); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, * denotes abundance category in PA is significantly higher than category outside PA, † denotes abundance category in PA is significantly lower than category outside PA after the application of Bonferonni corrections).

Table S4: Results of the Mann-Whitney U tests to compare the median abundance category of records inside PAs with the median abundance category of records outside PAs across species core ranges for the butterflies. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located outside PAs (nonPA) and inside PAs (PA); The mean abundance category for all records outside PAs (MeanNonPA) and inside PAs (MeanPA); the test statistic (W); the calculated effect size (effect, note that a negative effect size means the species is more abundant inside PAs than outside); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, * denotes abundance category in PA is significantly higher than category outside PA, † denotes abundance category in PA is significantly lower than category outside PA after the application of Bonferonni corrections).

Table S5: Results of the Mann-Whitney U tests to compare the median abundance category of records inside PAs with the median abundance category of records outside PAs across species core ranges for odonates. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located outside PAs (nonPA) and inside PAs (PA); The mean abundance category for all records outside PAs (MeanNonPA) and inside PAs (MeanPA); the test statistic (W); the calculated effect size (effect, note that a negative effect size means the species is more abundant inside PAs than outside); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, * denotes abundance category in PA is significantly higher than category outside PA, † denotes abundance category in PA is significantly lower than category outside PA after the application of Bonferonni corrections).

Table S6: Results of the Mann-Whitney U tests to compare the median abundance category of records inside PAs with the median abundance category of records outside PAs across species colonised ranges for the butterflies. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located outside PAs (nonPA) and inside PAs (PA); The mean abundance category for all records outside PAs (MeanNonPA) and inside PAs (MeanPA); the test statistic (W); the calculated effect size (effect, note that a negative effect size means the species is more abundant inside PAs than outside); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, * denotes abundance category in PA is significantly higher than category outside PA, † denotes abundance category in PA is significantly lower than category outside PA after the application of Bonferonni corrections).

Table S7: Results of the Mann-Whitney U tests to compare the median abundance category of records inside PAs with the median abundance category of records outside PAs across species colonised ranges for odonates. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located outside PAs (nonPA) and inside PAs (PA); The mean abundance category for all records outside PAs (MeanNonPA) and inside PAs (MeanPA); the test statistic (W); the calculated effect size (effect, note that a negative effect size means the species is more abundant inside PAs than outside); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, * denotes abundance category in PA is significantly higher than category outside PA, † denotes abundance category in PA is significantly lower than category outside PA after the application of Bonferonni corrections).

Table S8: Results of the Mann-Whitney U tests to compare the median abundance category of records in the core part of a species range with the median abundance category of records in the colonised part of a species range for the butterflies. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located in the core range (Core) and the colonised range (Col); The mean abundance category for all records in the core range (MeanCore) and in the colonised range (MeanCol); the test statistic (W); the calculated effect size (effect, note that a positive effect size means the species is more abundant in the core part of its range than the colonised part); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, ‡ denotes abundance category in the core range is significantly higher than in the colonised range, ▲ denotes abundance category in the core range is significantly lower than in the colonised range after the application of Bonferonni corrections).

Table S9: Results of the Mann-Whitney U tests to compare the median abundance category of records in the core part of a species range with the median abundance category of records in the colonised part of a species range for odonates. Column heading are as follows; the total number of locations with abundance records (N), the number of locations with abundance records located in the core range (Core) and the colonised range (Col); The mean abundance category for all records in the core range (MeanCore) and in the colonised range (MeanCol); the test statistic (W); the calculated effect size (effect, note that a positive effect size means the species is more abundant in the core part of its range than the colonised part); the 95% confidence interval of the effect size (confidence interval) and the significance level associated with the test (p-value, ‡ denotes abundance category in the core range is significantly higher than in the colonised range, ▲ denotes abundance category in the core range is significantly lower than in the colonised range after the application of Bonferonni corrections).

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