Supporting Information

Thomas et al. 10.1073/pnas.1210251109

SI Materials and Methods

Summary of Surveys and Ecological Information for the Seven Focal Species. The seven focal species were all of the species that met the criteria that they (*i*) were (previously) distributed in southern Britain and (*ii*) had been subjected to detailed repeated surveys and showed recent range expansions. In each case, data from the most recent survey had to have a spatial resolution of 1 ha or better, enabling us to analyze the association with protected areas (PAs), and had to be unbiased with respect to the conservation (PA) status of the land in question. Earlier formal surveys, combined with supplementary records, had to be sufficiently detailed so that we could be confident of absence in the earlier period. In surveys of focal species, the search rules to determine presence and absence were the same for PA and non-PA sites.

Each species exhibits climatic sensitivity, but the expansion of each species is likely to be a response to a number of environmental changes. The latter include past and recent management and restoration of habitats and, in the case of birds, the cessation of historic persecution contributes to their recent expansions. In this respect, they are typical of species expanding (and infilling) their distributions near their cool northern-range boundaries, showing impacts of the separate, combined, and/or potentially interacting effects of climate and other constraints.

Butterfly Species. The two butterfly species included have been subject to patch-based repeat surveys using systematic survey methodology (1). They occur in some of the most heavily recorded landscapes for butterflies in Britain, which supplement formal survey data (2, 3), ensuring that the distribution was fully known in the earlier time periods (4, 5).

Hesperia comma. The silver-spotted skipper inhabits dry (calcareous) grasslands in southern England, where adults are conspicuous when nectaring and sitting on paths, which they frequently do while thermoregulating. The eggs are extremely easy to find by practiced surveyors, because they are highly visible among the very fine leaves of the grass species, *Festuca ovina*, on which they are laid. *H. comma* used to be restricted to particularly hot microclimates, inhabiting sparsely vegetated *F. ovina* grasslands (hence, they benefitted from habitat management that creates these hot microclimates) on south-facing hillsides, but they have responded to regional warming by colonizing a wider range of aspects (west, east, and north) and denser vegetation, as well as expanding its regional distribution (6, 7). A complete national survey of all sites known to be occupied between 1950 and 1980 was carried out in 1982, searching all similar calcareous grassland habitats and locations (irrespective of site designation) within a radius of ~10 km; this information was supplemented by additional surveys of Dorset and surrounding areas in 1978 and Wiltshire in 1983 and 1984 (8). The national distribution of this species was highly localized as well as occurring in some of the best-recorded landscapes for butterflies in southern Britain (2, 3), making it extremely unlikely that undiscovered colonies existed on other PAs at that time. A survey of the North and South Downs hills was carried out in 1991, searching all calcareous grassland habitats within 10 km of a 1982 colony and then extending the survey to within 10 km of any new colony found in 1991, again irrespective of the conservation designation of habitat patches (9). The 1991 survey also included extensive surveys (sample surveys in patches a few kilometers apart throughout the region); no new colonies were found in the extensive zone either during the survey itself or in the records of the national dataset held by the Biological Records Centre from 1985 to 1991, indicating that the range expansion was well-characterized.

Another full national survey was carried out by 10 trained researchers in 2000, and it was followed up by partial surveys in 2001/2002 searching calcareous grassland locations irrespective of protected area status. This survey extended to all sites within 15 km of populations of the species recorded by censuses in 1995–1999 for the national distribution atlas (2) or any of the previous surveys (6, 10). Whenever a new site was located by adult or egg searches, the survey was extended to 15 km away. Given the relatively short dispersal (11) and colonization distances (6–8) of *H. comma* and the high detectability of eggs in addition to adult records, the surveys are likely to have been virtually exhaustive. Six figure national ordnance survey grid references (1-ha resolution) were recorded for the centers of each occupied habitat patch. Conservation designation was not a survey criterion at any point, so recorded colonizations are unbiased with respect to PAs.

Polyommatus (Lysandra) bellargus. The Adonis blue also inhabits unimproved calcareous grasslands, where its sole host plant, *Hippocrepis comosa*, is extremely conspicuous, especially when in flower. The brilliantly colored male Adonis blues frequently aggregate in sheltered locations near the base of calcareous hillsides, making this species one of the most conspicuous (as well as prized by amateur recorders) butterfly species in Britain. Both males and females fly and nectar across their grassland habitats, and eggs may be found on *H. comosa* plants of appropriate growth form; the butterflies rarely stray from their local habitat patch (12). This butterfly is temperature-sensitive and thermally limited in Britain, with an estimated doubling of resource availability at warm times of year, enabling it to benefit from warm years as well as habitat management that generates warm microclimates (13). This species was surveyed intensively on two occasions in the county of Dorset and in south Wiltshire; both areas are within one of the best-recorded regions of England for butterflies (14–16) and the stronghold of this species in Britain, supporting >50% of all British populations (3, 12). The first survey was carried out in both adult generations in 1978 (12), building on previous surveys (17), data from the Biological Records Centre, and correspondence with individual entomologists together with a complete inventory of grasslands that contained *H. comosa* obtained from comprehensive Nature Conservancy Council surveys. All locations with previous records were visited, and nearby potential grassland habitats containing host plants, irrespective of PA designation, were also visited. A full resurvey was carried out in 1999, again searching all potential (*H. comosa*-containing grassland) sites in the same region irrespective of conservation status (18). Six figure national ordnance survey grid references (1-ha resolution) were recorded for the centers of each habitat patch.

Bird Species. The five bird species included in this analysis all had distributions heavily biased to the south of Britain in the period from 1988 to 1991, corresponding to the second national survey of the distributions of breeding birds in Britain (19). This Survey aimed to identify all 10 × 10-km (100 km^2) resolution Ordnance Survey grid squares within which breeding took place, providing baseline distributions. These atlas records were supplemented by specific individual surveys, which took place before or at the same time as the atlas survey. We deem colonizations to be any sites colonized subsequently outside of the grid squares occupied in 1988–1991, including all data from 1992 on collected during species-specific surveys. The species-specific surveys recorded

breeding activity at 1-ha resolution, taking "probable"(e.g., carrying nesting material) and "confirmed" breeding activities, as defined for each species, as evidence of presence.

Botaurus stellaris. Despite the visually cryptic nature of bitterns, the deep, booming, and far-carrying call of male bitterns makes this species virtually impossible to miss at its breeding sites. These sites are in *Phragmites australis* reedbeds, a highly fragmented and restricted habitat that is well-described and visited by bird recorders in Britain. The Eurasian Bittern *Botaurus stellaris* was extirpated from Britain by a combination of habitat loss and persecution by the late 1880s, a period when the climate was also relatively cold. After recolonization in the early decades of the 20th century, the population initially grew and then declined again to 11 males in 1997, by which time many reedbeds had dried out and became unsuitable (20, 21). Survival is positively related to winter rainfall (22), which in turn is correlated with winter warmth (23). In contrast, bitterns struggle to find food (reducing body condition) when wetlands freeze solid in winter (24, 25), although it is not known how freezing affects survival or subsequent breeding success. The remaining bittern strongholds were in freshwater wetlands on the coast of East Anglia, where they are increasingly at risk from inundation by sea water during storms (which climate change models predict will increase in severity and frequency), leading to a major push by conservationists to restore reedbed habitats at inland sites. Annual surveys of male bitterns at all suitable reedbeds have been coordinated by Royal Society for the Protection of Birds (RSPB) and Natural England since 1990, with more intensive survey work since 1994, to monitor numbers of nesting females and booming males (24, 25) and describe the species' ecological requirements. Only those males that are known to have boomed for 1 wk or more are counted in the minimum figures for the year. Where a site or area holds or is thought to hold more than one boomer, the number of boomers actually involved is confirmed by hearing different boomers at the same time and comparing the booming periods of each male to confirm that they overlap. Population recovery to 104 males in 2011 has taken place during a period of increased winter precipitation and warmth (23), and it was facilitated by wetland restoration, creation, and appropriate management in southern England (24, 25). Hence, there is near-complete knowledge of the recent range expansion of this species from 7 to 51 sites.

Burhinus oedicnemus. The stone curlew is a summer visitor (March to October), breeding mainly in areas characterized by relatively low precipitation and having a tendency to aridity: it reaches the northern edge of its geographic distribution in England and is predicted to increase in southeast England in response to climate change (26). It occupies hot and dry microhabitat types in England, mainly the seminatural short grassland (42% of nesting attempts) and tilled arable habitats on free-draining sandy soils (27, 28). The birds feed on arthropods and earthworms, particularly at night and around dawn and dusk. The population suffered a long-term decline to less than 170 pairs by 1991 as a result of the loss of seminatural grassland habitats and high egg and chick mortality on farmland as a result of agricultural operations (29). In response, research and detailed monitoring have been carried out since the mid-1980s and involved an intensive color-ringing scheme and high reporting by local ornithologists as well as systematic searches by professional surveyors. Despite the bird's nocturnal habits and secretive behavior, it can be surveyed using nocturnal playback of taped calls and daytime searches, with some 80–90% of pairs detected each year estimated from the resighting of marked individuals (2, 30). Recent expansion to 369 pairs (by 2010) was facilitated by the physical protection of nests from agricultural machinery on farmland and the uptake of agrienvironment schemes that provide the sparse microhabitats (warm microclimates) selected by nesting birds (28, 31, 32). This species' expansion is not strongly associated with Sites of Special Scientific Interest-designated PAs (Table 1), but its expansion is, nonetheless, associated with specific conservation actions outside PAs: legal protection to nesting birds associated with its status as a schedule 1 species under the Wildlife and Countryside Act 1981 and agrienvironment schemes that help generate suitable habitats through conservation easement rather than PA designation.

Caprimulgus europaeus. The European nightjar is a nocturnal insectivore that catches flying insects on the wing. It is a summer visitor to Europe, breeding principally where the annual temperature sum is between ∼1,000 and 3,500 degree d above 5 °C and seasonal moisture deficiency is moderate to slight, giving a projected increase in the climatic suitability of Britain for nightjar under climate change (26). It is also affected by nonclimatic changes to the environment. The population in the United Kingdom halved and contracted in range between the 1950s and 1970s (19), a change that coincided with detrimental land use changes, particularly the loss of heathlands, as well as slight cooling (deterioration) of the climate in the 1950s and 1960s; these losses were particularly severe in the relatively cold and wet north and west, at the species' climatic range margins. As a result of this decline, the nightjar has been the subject of 1-km^2 resolution national surveys, which took place in 1981, 1992, and 2004 using nocturnal surveys to record displaying males, most of which are associated with heathland or open woodland habitats (33–36). The birds are easily detected by their churring song and other calls (they respond to tape recordings and humans mimicking them). Coverage of potentially suitable habitat is estimated to be high (at around 80%). Surveys follow a stratified random sampling of suitable potential habitats (defined by vegetation type and not PA status) in core and marginal regions. The population has increased from a low of 2,100 males in 1981 to 4,100 in 2004, again associated with a more favorable combination of habitat and climatic changes: altered forestry practices, habitat protection and restoration, and warmer summers (33, 37, 38).

Lullula arborea. The woodlark breeds in Europe and reaches its northwestern range limit in the south and east of England. It mainly occurs where the annual temperature sum is above ∼1,200 degree d above 5 °C and the coldest month mean temperature is above about −10.5 °C; southern Britain is predicted to show increased climate suitability for this species under climate change (26). Apparent population declines since 1970 sparked concern over the status of this species, and hence the woodlark has been subject to national surveys in 1986, 1997, and 2006 (39–41). These surveys have documented a recent population increase and range expansion from 241 pairs in 1986 to 3,064 pairs in 2006, with 67% of pairs associated with heathland and 32% of pairs associated with woodland in 2006. All historic sites that still contain potential suitable habitat were surveyed, having been identified by previous surveys, atlases, and other bird recorders. Potentially suitable habitats were heathland, young plantations, and habitat with free-draining soils; around 10% of historic sites were wholly unsuitable because of land use changes, and hence they were not surveyed for birds. In addition, a random sample of habitat (irrespective of PA designation) was surveyed within a 5-km buffer (75% sampled) and 5- to 10-km buffer (25% sampled) of occupied sites. About one-third of territories were estimated to occur in the 5-km buffer, but none of territories occurred in the 5- to 10-km buffer, suggesting that the range expansion has been well-characterized (39). The recent expansion is associated with increased habitat protection and management, particularly the increased creation and maintenance of warm, early successional conditions within forests; numbers also vary with levels of predation (42). The species is likely to be limited by winter mortality during cold weather, and it may benefit from increasing summer temperatures (38); females lay larger clutches during warm and dry springs, nest success in-

creases with temperature, and fledging success per egg is higher under drier conditions (42).

Sylvia undata. The Dartford warbler is an insectivore that is resident in the United Kingdom, where it is associated with lowland heathland. It is cold-sensitive and has a range limit delimited by an isotherm where the mean temperature of the coldest month exceeds 2 °C; hence, Britain is predicted to become far more suitable for this species under climate change (26). As a result of this cold sensitivity, the species came close to extinction in Britain after the severe winter of 1962–1963. Given its restricted range and high habitat specificity (96% of territories associated with heathland) (43), the species has been well-monitored by both bird recorders and four national standardized surveys (44). Core sites where the species is known to occur are intensively covered, and there is also high-intensity sampling of a stratified random sample of 1-km squares in 5- and 5- to 10-km buffers around existing sites to describe potential range expansion and colonization of new sites (43, 45–47). These surveys have documented a substantial population increase and range expansion from 1974 to 2006, in response to milder winters. Increasing temperatures have been shown to have facilitated an expansion of the altitudinal range of this species (44).

Supplementary Analyses of Invertebrate Species. ***Analysis of comparator species.*** For 251 of 256 colonizing invertebrate species, we were able to identify resident (present in both the first and second recording periods) comparator species that were already present in the regions being colonized (defined as the 25% of species from the same taxonomic group that occupied the largest number of 10 × 10-km squares in the first recording period) to represent the distribution of biological recording in these regions. We only included 10 × 10-km colonization squares that contained comparator species records in both periods. We calculated the overall PA use of comparator species (i.e., fraction of 100 × 100-m resolution records falling within PAs) in the 10 × 10-km squares colonized by each of the 251 species separately. We then compared the PA use ratio of each colonizing species with the combined PA use ratio of its comparator residents. Colonizing species were significantly more strongly associated with PAs than their comparator residents: 170 (67.7%) species for which comparator residents were available were more strongly associated with PAs than the preexisting residents (Wilcoxon signed rank test, $v = 22{,}305$, $P < 0.0001$). This test may be conservative, because widespread (generalist butterfly) species tend to be more numerous on PAs than nearby non-PA farmland (48), and they are somewhat more frequently observed on PAs than elsewhere (Fig. 4).

Analysis of recording events. Most of the colonizations reported here took place in southern Britain, which has been subject to intensive volunteer and professional biological recording during the period considered; it is, perhaps, the best-recorded region of the world. Every 10-km resolution grid square in this region has been visited by biological recorders on tens or, in most cases, hundreds of occasions, and therefore we have high levels of confidence in the overall patterns of change. Although there were 121,517 unique (after removing duplicates) 1-ha resolution colonization records for the colonizing invertebrate species, not every 1-ha resolution has been recorded within the invertebrate databases. Therefore, we carried out an additional analysis considering only those 1-ha resolution locations that had definitely been visited by biological recorders. We know where these locations are because the locations and dates of records are documented within the biological databases themselves. We defined recording events as locations and times where there was direct evidence—from distributional data—that recorders had visited and recorded species of a given taxonomic group. For this analysis, we only considered multispecies recording events, which were defined as date- (single day) and location- (1-ha resolution grid reference) specific sets of records for species of a particular taxonomic group. Only events with three or more species recorded were included to make sure that recorders were recording species in general and, hence, would have been expected to report the presence of any other species of the same taxonomic group seen at the same time and place. We selected one event at random for any 1-ha location that was recorded on more than one occasion. For each species, we calculated (*i*) the fraction of PA in locations where recording events revealed presence and (*ii*) the fraction of PA in locations where documented recording events did not reveal the same species. We then compared these two fractions. This calculation confirmed that species were still disproportionately associated with PAs for the subset of 1-ha resolution data for which there was definitive evidence that biological recording had taken place (Wilcoxon signed rank test, $n = 242$ species, $v = 19{,}400$, $P < 0.0001$).

1. Thomas JA (1983) A quick method for estimating butterfly numbers during surveys. *Biol Conserv* 27:195–211.
2. Asher J, et al. (2001) *The Millennium Atlas of Butterflies in Britain and Ireland* (Oxford Univ Press, Oxford).
3. Heath J, Pollard E, Thomas JA (1984) *Atlas of Butterflies in Britain and Ireland* (Viking, Harmandsworth).
4. Thomas JA, et al. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* 303:1879–1881.
5. Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philos Trans R Soc Lond B Biol Sci* 360: 339–357.
6. Thomas CD, et al. (2001) Ecological and evolutionary processes at expanding range margins. *Nature* 411:577–581.
7. Davies ZG, Wilson RJ, Coles S, Thomas CD (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *J Anim Ecol* 75:247–256.
8. Thomas JA, Thomas CD, Simcox DJ, Clarke RT (1986) The ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. *J Appl Ecol* 23: 365–380.
9. Thomas CD, Jones TM (1993) Partial recovery of a skipper butterfly (*Hesperia comma*) from population refuges: Lessons for conservation in a fragmented landscape. *J Anim Ecol* 62:472–481.
10. Davies ZG, Wilson RJ, Brereton TM, Thomas CD (2005) The re-expansion and improving status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain: A metapopulation success story. *Biol Conserv* 124:189–198.
11. Hill JK, Thomas CD, Lewis OT (1996) Effects of habitat patch size and isolation on dispersal by Hesperia comma butterflies: Implications for metapopulation structure. *J Anim Ecol* 65:725–735.
12. Thomas JA (1983) The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae) in Britain. *J Appl Ecol* 20:59–83.
13. Roy DB, Thomas JA (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. *Oecologia* 134:439–444.
14. Thomas J, Webb N (1984) *Butterflies of Dorset* (Dorset Natural History and Archaeological Society, Dorchester, United Kingdom).
15. Fuller M (1995) *The Butterflies of Wiltshire* (Pisces Publications, Newbury).
16. Thomas J, Surry R, Shreeves B, Steele C (1998) *New Atlas of Dorset Butterflies* (Dorset Natural History and Archaeological Society, Dorchester, United Kingdom).
17. Buxton RD, Connolly ML (1973) *1973 Survey of the Adonis Blue, Lysandra bellargus Rott. Report to the Joint Committee for the Conservation of British Insects* (Joint Committee for the Conservation of British Insects, London).
18. Thomas JA, et al. (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proc Biol Sci* 268:1791–1796.
19. Gibbons DW, Reid JB, Chapman RA (1993) *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991* (T. & A. D. Poyser, Berkhamsted).
20. Gilbert G, Painter M, Smith KW (1996) An inventory of British reedbeds in 1993. *RSPB Conserv Rev* 10:39–45.
21. Tyler GA, Smith KW, Burgess DJ (1998) Reedbed management and breeding Bitterns *Botaurus stellaris* in the UK. *Biol Conserv* 86:257–266.
22. Gilbert G, Tyler GA, Smith KW (2002) Local annual survival of booming male Great Bittern *Botaurus stellaris* in Britain, in the period 1990–1999. *Ibis* 144:51–61.
23. Perry M (2006) *A Spatial Analysis of Trends in the UK Climate Since 1914 Using Gridded Datasets. National Climate Information Centre Climate Memorandum No 21* (Meteorological Office, Exeter, United Kingdom).
24. Wotton S, McIntyre R, Schmitt S, Gregory R, Brown A (2012) *Bittern* Botaurus stellaris *Monitoring in the UK: Summary of the 2011 Season* (RSPB, Sandy).
25. Brown A, Gilbert G, Wotton S (2012) Bitterns and bittern conservation in the UK. *Br Birds* 105:58–87.
26. Huntley B, Green RE, Collingham YC, Willis SG (2007) *A Climatic Atlas of European Breeding Birds* (Lynx Edicions, Barcelona).

27. Green RE, Tyler GA, Bowden CGR (2000) Habitat selection, ranging behaviour and diet of the stone curlew (*Burhinus oedicnemus*) in southern England. *J Zool* 250:161–183.
28. Aebischer NJ, Green RE, Evans AD (2000) From science to recovery: Four case studies of how research has been translated into conservation action in the UK. *Ecology and Conservation of Lowland Farmland Birds*, eds Aebischer NJ, Evans AD, Grice PV, Vickery JA (British Ornithologists' Union, Tring), pp 43–54.
29. Green RE (1988) Stone curlew conservation. *RSPB Conserv Rev* 2:30–33.
30. Green RE (1995) Monitoring of stone curlew numbers and breeding success. *Britain's Birds in 1991–92: The Conservation and Monitoring Review. BTO & JNCC*, ed Carter SP (Thetford, United Kingdom).
31. Evans AD, Green RE (2007) An example of a two-tiered agri-environment scheme designed to deliver effectively the ecological requirements of both localized and widespread bird species in England. *J Ornithol* 148:S279–S288.
32. Eaton MA, et al. (2011) *The State of the UK's Birds 2011* (RSPB, BTO, WWT, CCW, JNCC, NE, NEIA and SNH, Sandy).
33. Conway G, et al. (2007) Status and distribution of European nightjars *Caprimulgus europaeus* in the UK in 2004. *Bird Study* 54:98–111.
34. Gribble F (1983) Nightjars in Britain and Ireland in 1981. *Bird Study* 30:157–176.
35. Morris A, Burges D, Fuller RJ, Evans AD, Smith KW (1994) The status and distribution of Nightjars *Caprimulgus europaeus* in Britain in 1992. *Bird Study* 41:181–191.
36. Conway C, et al. (2007) Status and distribution of European Nightjars *Caprimulgus europaeus* in the UK in 2004. *Bird Study* 54:98–111.
37. Green RE, Harley M, Spalding M, Zöckler C (2001) *Impacts of Climate Change on Wildlife* (RSPB, Sandy).
38. Langston RHW, et al. (2007) Nightjar *Caprimulgus europaeus* and woodlark *Lullula arborea*—recovering species in Britain? *Ibis (Lond 1859)* S149:250–260.
39. Conway G, et al. (2009) The status of breeding woodlarks *Lullula arborea* in Britain in 2006. *Bird Study* 56:310–325.
40. Sitters HP (1986) Woodlarks in Britain, 1968–83. *Br Birds* 79:105–116.
41. Wotton SR, Gillings S (2000) The status of breeding Woodlarks *Lullula arborea* in Britain in 1997. *Bird Study* 47:212–224.
42. Wright LJ, et al. (2009) Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark *Lullula arborea*. *J Anim Ecol* 78:1191–1202.
43. Wotton S, Conway G, Eaton M, Henderson I, Grice P (2009) The status of the Dartford Warbler in the UK and Channel Islands in 2006. *Br Birds* 102:230–246.
44. Bradbury RB, Pearce-Higgins JW, Wotton SR, Conway GJ, Grice PV (2011) The influence of climate and topography in patterns of territory establishment in a range-expanding bird. *Ibis* 153:336–344.
45. Bibby CJ, Tubbs CR (1975) Status, habitats and conservation of the Dartford Warbler in England. *Br Birds* 68:177–195.
46. Robins M, Bibby CJ (1985) Dartford Warblers in 1984 Britain. *Br Birds* 78: 269–280.
47. Gibbons DW, Wotton S (1996) The Dartford Warbler in the United Kingdom in 1994. *Br Birds* 89:203–212.
48. Hodgson JA, Kunin WE, Thomas CD, Benton TG, Gabriel D (2010) Comparing organic farming and land sparing: Optimizing yield and butterfly populations at a landscape scale. *Ecol Lett* 13:1358–1367.