by the hatching success for each host, and then calculated the fraction of all ducklings hatching in nests of each host.

Assessing costs to hosts

When assessing whether the presence of duck eggs increased the risk of nest predation for hosts, we excluded parasitized nests in which all duck eggs were rejected. Nests were considered preyed on if all eggs disappeared before they were due to hatch or if we had clear evidence for predation (broken eggs). Clutch size varies considerably between individual hosts, so we assessed hatching success in terms of the number of host eggs that failed to hatch at each nest; this measure includes eggs that disappeared, were rejected or were left over after the rest hatched. Leftover or rejected host eggs were rare, so we primarily measured egg loss. Our more detailed analysis of egg loss in red-fronted coots included experimental nests from which real parasitic eggs were removed quickly after laying ($n = 25$) or in which parasitic duck eggs were experimentally added to unparasitized nests ($n = 22$); these two types of experimental nest enabled us to decouple egg loss due to the act of parasitism itself (damage or removal by parasite) from egg loss due to the presence of duck eggs itself, such as damage to host eggs with subsequent removal by hosts[19]. The latter cost favours egg rejection; the former does not.

Mimicry experiments

The white, oval-shaped duck eggs differ from the host eggs in three key visual features—rounder shape, paler background colour and lack of spots (Figs 1h and 2a). We painted domestic chicken eggs and real host eggs to create a series of three egg treatments that increasingly resembled host eggs—the least mimetic 'white duck' eggs (experimental versions of real duck eggs) had the wrong shape, background colour and lacked spots, whereas the most mimetic 'brown coot' eggs lacked only spots (Fig. 2a). Egg colour and shape vary in real duck eggs (although to a much smaller degree), so these should be feasible evolutionary steps towards mimicry. To avoid a confounding effect of size, we used painted red-gartered coot eggs for the 'brown coot' treatment for both hosts, because this species overlaps in size with the duck eggs. For the 'brown duck' and 'white duck' treatments we used chicken eggs whose length and width both overlapped with those of real duck eggs. We added the experimental eggs to host nests in the laying or early incubation stages and we determined their fates in subsequent visits. Eggs were scored as rejected if found buried in the nest or if observed at least half buried on the final nest visit for nests that hatched or were preyed on before rejection was complete. Non-rejected eggs were scored as accepted only if the nest remained active long enough for rejection to have occurred (at least 10 days for both species).

Intraspecific brood parasitism

In 1997 our studies were conducted primarily on open wetlands where red-fronted coots were absent, so our detailed analysis of intraspecific brood parasitism is restricted to red-gartered coots. Nests were checked every two to four days, which will underestimate parasitism on the basis of unusual egg-laying rates (two or more new eggs per day)[28], so we focused on variation in egg features, a reliable method when used conservatively[29]. Our retrospective assessment of intraspecific brood parasitism from the earlier field seasons, where we did not specifically focus on detecting intraspecific brood parasitism, will greatly underestimate the actual rate of intraspecific brood parasitism: nest checks were relatively infrequent and we would have noticed only the most extreme cases of variation in egg features to detect parasitism[28–30].

Received 20 July; accepted 13 September 2004; doi:10.1038/nature03036.

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Acknowledgements We thank C. Benkman, J. Briskie, A. Chaine, N. Davies, M. Hauber, A. Lotem, D. Mock, R. Montgomerie, S. Rothstein, J. Thompson and K. Wasson for comments on the manuscript; the National Geographic Society and the British Broadcasting Corporation (D. Attenborough's *Life of Birds*) for funding; the Flores family, J. Echerran, M. Beade and J. C. Reboreda for logistic support; and V. Meuhter, G. Goggin and A. Carminati for assistance in the field. During part of the study, B.E.L. was supported by the Kananaskis Field Stations of the University of Calgary and University of California, and J.McA.E. by the Dennis G. Raveling Endowment.

Competing interests statement The authors declare that they have no competing financial interests.

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Spatial patterns in species distributions reveal biodiversity change

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Interpretation of global biodiversity change is hampered by a lack of information on the historical status of most species in most parts of the world[1–5]. Here we show that declines and increases can be deduced from current species distributions alone, using spatial patterns of occupancy combined with distribution size. Declining species show sparse, fragmented distributions for their distribution size, reflecting the extinction process; expanding species show denser, more aggregated distributions, reflecting colonization. Past distribution size changes for British butterflies were deduced successfully from current distributions, and former distributions had some power to predict future change. What is more, the relationship between distribution pattern and change in British butterflies

independently predicted distribution change for butterfly species in Flanders, Belgium, and distribution change in British rare plant species is similarly related to spatial distribution pattern. This link between current distribution patterns and processes of distribution change could be used to assess relative levels of threat facing different species, even for regions and taxa lacking detailed historical and ecological information.

Biodiversity assessment relies heavily on combining information on current species status with rates of decline or increase[1–8]. However, direct evidence of change is unavailable for most taxonomic groups, and for most parts of the world. It is possible to list species as internationally threatened if they have extremely small distribution sizes or population sizes[4,6,8], but rates of decline might better identify levels of threat facing different species, and ignorance of rates of decline might lead to underestimates of extinction risk[1,3]. Furthermore, species whose distributions have been recorded at finer scales are more likely to meet criteria for listing based on small distribution size[3,6,9]. Red Data Books are therefore dominated by well-known taxa in well-known regions, even though less well documented groups may be equally endangered and indeed are usually more species-rich than better-known taxa[2,5]. Here we evaluate whether levels of decline or increase can be deduced from current status alone, because past colonization and extinction processes leave different spatial signatures on species' distribution patterns. Declining species are expected to have sparse distributions because extinctions cause retractions in range to optimal habitats[10–12] or to locations that have been least affected by wide-acting extinction forces[13]. Increasing species are expected to have more aggregated distributions, resulting from distance-delimited colonization processes[14].

Butterflies form the model system. In Britain, butterfly distributions were mapped comprehensively at 10 km resolution in 1970–82 (ref. 15) and 1995–99 (ref. 16), allowing the measurement of declines and increases[17] and the analysis of spatial distribution patterns. Fine-scale (10-km) distribution records for some species are aggregated in relatively few coarse-scale (100-km) cells (Fig. 1a, b), whereas fine-scale records for other species are scattered sparsely over a wider range of coarse-scale cells (Fig. 1c, d). To quantify this pattern for each species' distribution, we summed first the total area of occupied 10-km cells, and second the total area of occupied 100-km cells, and plotted the logarithm of the area of occupancy (AOO) at each scale against the logarithm of the side of the grid cell (Fig. 1e, f). The slope of this scale–area curve[18] (or range–area relationship[19]) gives a measure of the aggregation of each species' distribution (the fractal dimension, D_{ij})[6,18]. In the most aggregated distributions, a maximum value of $D_{ij} = 2$ indicates that occupied fine-scale cells completely fill each occupied coarse-scale cell. In the sparsest distributions, a minimum value of $D_{ij} = 0$ indicates that each occupied fine-scale cell is located in a separate coarse-scale cell.

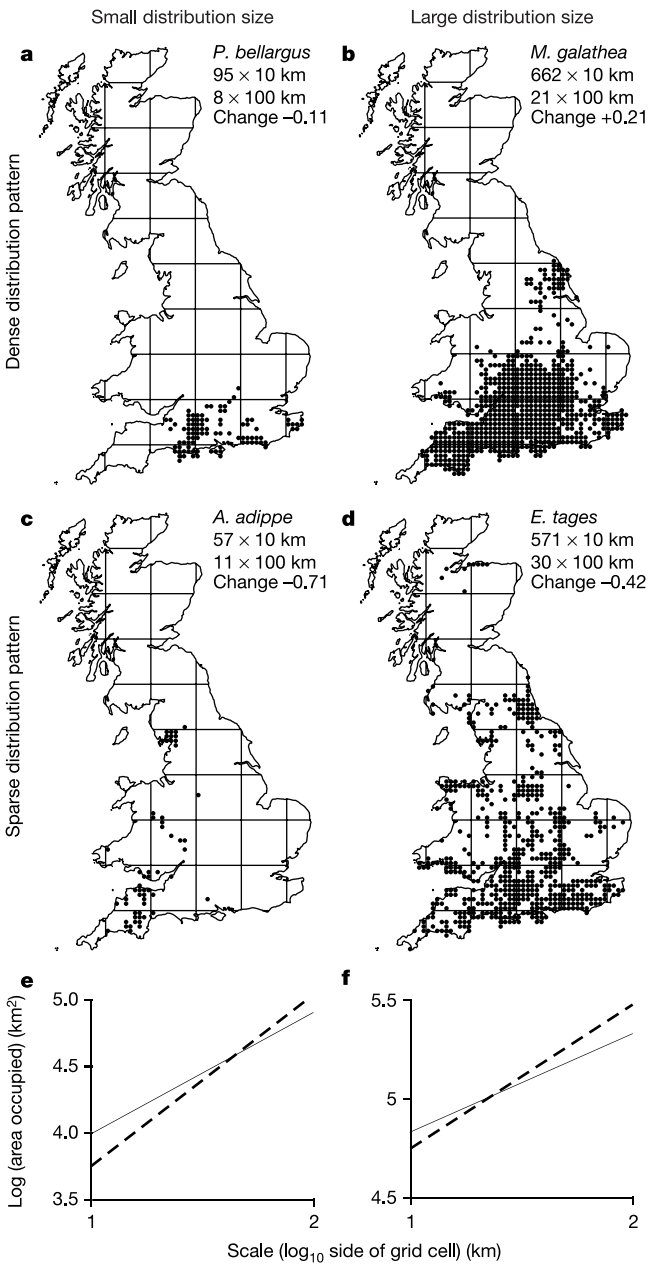

Figure 1 Maps and associated scale–area curves for 1995–99 distributions of British butterfly species. **a**–**d**, Distribution maps at 10 km resolution, showing the number of 10-km and 100-km cells occupied, and proportional change in 10-km records since 1970–82. **a**, *Polyommatus bellargus*, small, dense distribution; **b**, *Melanargia galathea*, large, dense distribution; **c**, *Argynnis adippe*, small, sparse distribution; **d**, *Erynnis tages*, large, sparse distribution. **e**, **f**, Plots of $\log_{10}$(area occupied) against scale ($\log_{10}$(side of distribution grid cell)) for *P. bellargus* (solid line) and *A. adippe* (dashed line) (**e**), and *M. galathea* (solid line) and *E. tages* (dashed line) (**f**). Note difference in occupancy (*y*-axis) values between **e** and **f**. Sparsely distributed species show steeper scale–area curves.

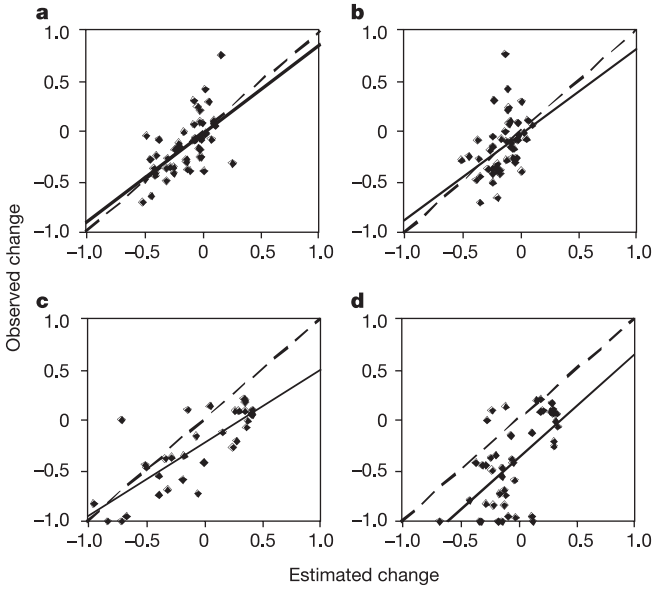

Figure 2 Observed changes in distribution size against changes estimated from distribution pattern and size. **a**, Deductions of past change from 1995–99 distributions in Britain. **b**, Predictions of future change from 1970–82 distributions in Britain. **c**, Deductions of past change from 1991–99 distributions in Flanders. **d**, Predictions of future change from pre-1991 distributions in Flanders. Solid lines are regressions; dashed lines indicate equality of observations and estimations.

Regressions of change in butterfly distribution size (1970–82 to 1995–99) against 1995–99 distribution size at 10 km resolution ($R^2 = 0.16$, $F_{1,49} = 9.53$, $P = 0.003$; change = 0.18AOO − 0.97) or fractal dimension ($R^2 = 0.32$, $F_{1,49} = 23.13$, $P < 0.001$; change = $0.48D_{ij} - 0.79$) showed that species with large or aggregated distributions had increased more than species with small or sparse distributions. However, D_{ij} is positively related to AOO ($R^2 = 0.86$, $F_{1,49} = 307.3$, $P < 0.001$), and analysing both variables together showed that species with aggregated distributions for their distribution size had increased the most, whereas species with sparse distributions for their distribution size had declined ($R^2 = 0.43$, $F_{2,48} = 18.06$, $P < 0.001$; change = $0.08 + 1.18D_{ij} - 0.39$AOO). To determine whether changes in distribution size could be deduced without knowledge of a species' former distribution, simply by examining its current distribution pattern, each species in turn was omitted from the analysis, and the regression of change against D_{ij} and AOO for the remaining species was used to estimate change for the omitted species. These independent deductions of distribution change accounted for 37–38% of variation in observed changes in distribution size (Fig. 2a; $R^2 = 0.38$, $F_{1,49} = 29.77$, $P < 0.001$; observed change = 0.89 (±s.e.m. 0.16) × estimated change − 0.02 (±s.e.m. 0.04); $R^2 = 0.37$ from phylogenetic generalized least squares (GLS) regression).

To be useful for biodiversity assessment, the relationship of distribution change to spatial distribution pattern should be robust to the nature and quality of distribution data. For British butterflies, the combined ability of distribution pattern and size to deduce distribution change remained strong even if data on change were only available for a small fraction of species (using information from ten randomly selected species to predict change in the remaining 41 species, R^2 ranged from 0.30 to 0.45; Supplementary Information). D_{ij} calculated over a range of scales between 10 and 100 km ranked species consistently (Supplementary Table 3), and the relationship of distribution change with D_{ij} and AOO was consistent, although it was strongest with finer-resolution data (Supplementary Table 4). Neither mobility nor population density was significantly related to the unexplained variation in distribution change (Supplementary Methods), further suggesting that the level of variation explained stems more from data quality than from effects of other explanatory variables.

To test the robustness of the relationship to the method used to quantify aggregation, we also calculated two statistics, D_x (ref. 20) and Ripley's L (ref. 21), on the basis of the number of conspecific records in circles of different-sized radii (10, 20, 50 and 100 km) around each distribution record. In each case, distribution change was positively related to the aggregation of species' distributions relative to their size. The two methods explained similar proportions of variation to that explained by D_{ij} (R^2 for observed change against D_x and AOO ranged from 0.47 to 0.54 at the different scales; for Ripley's L and AOO, R^2 ranged from 0.23 to 0.39) (Supplementary Information).

Species may show time lags in their declines to extinction in fragmented landscapes[22] and in their colonization of regions that have become suitable[23], such that past distribution patterns may show the beginnings of range contractions or expansions, and may have some power to predict future change. Distribution change in British butterflies from 1970–82 to 1995–99 was significantly related to fractal dimension and area of occupancy in 1970–82 ($R^2 = 0.23$, $F_{2,48} = 7.32$, $P = 0.002$; change = $0.40 + 1.18D_{ij} - 0.44$AOO), but 1970–82 distribution pattern and size independently predicted a lower proportion of variation in species' future declines and increases when each species was omitted in turn from the analysis (Fig. 2b; $R^2 = 0.18$, $F_{1,49} = 10.47$, $P = 0.002$; observed change = 0.85 (±s.e.m. 0.26) × estimated change − 0.02 (±s.e.m. 0.05); phylogenetic GLS $R^2 = 0.16$). The reduced power of the predictions of future change, compared with the deductions of past change, probably result from the earlier survey's less-detailed distribution data, and because processes of range expansion and contraction themselves lead to pronounced differences in aggregation. Between the two surveys, the distributions of expanding species became more aggregated, and those of contracting species more fragmented, because the residuals for most declining species from the regression of D_{ij} against AOO declined from 1970–82 to 1995–99, whereas the residuals for expanding species increased ($R^2 = 0.10$, $F_{1,49} = 5.70$, $P = 0.02$; distribution change = −0.15 (±s.e.m. 0.04) + 1.24 (±s.e.m. 0.52) × change in residuals). Processes of distribution change may increase fragmentation in the distributions of already declining species, increasing their risk of future decline by reducing colonization rates and increasing rates of local extinction[24]. Although predictions of change from the earlier survey were less powerful than deductions from the later survey, the combination of distribution pattern and size still explained two to three times as much variation (16–18%) as the 6–7% explained by distribution size alone ($R^2 = 0.07$, $F_{1,49} = 3.59$, $P = 0.06$; observed change = 0.12AOO − 0.70; phylogenetic GLS $R^2 = 0.06$). It therefore does seem possible to predict future dynamics from current species distributions, although additional refinements might be required before such forecasting can be applied directly to conservation.

The potential of this approach for biodiversity assessment is supported by tests of the relationship for another landscape and another taxonomic group. As a test of sensitivity to landscape, the relationship of distribution change with distribution pattern and size in British butterflies was used to deduce changes in the distributions of butterflies in Flanders, Belgium, that have been mapped at 5-km scale in two date categories, pre-1991 and 1991–99 (ref. 25). The British relationship of change with 1995–99 distributions, combined with D_{ij} and AOO for Flanders butterflies in 1991–99, successfully deduced changes in distribution size in Flanders (Fig. 2c; $R^2 = 0.65$, $F_{1,32} = 58.82$, $P < 0.001$; observed change = 0.73 (±s.e.m. 0.10) × estimated change − 0.23 (±s.e.m. 0.04); phylogenetic GLS $R^2 = 0.64$). Similarly, the British relationship of change with 1970–82 distributions, combined with pre-1991 D_{ij} and AOO for Flanders, significantly predicted future changes in Flanders (Fig. 2d; $R^2 = 0.36$, $F_{1,32} = 18.18$, $P < 0.001$; observed change = 1.00 (±s.e.m. 0.23) × estimated change − 0.30 (±s.e.m. 0.05); phylogenetic GLS $R^2 = 0.37$) (Supplementary Methods). Flanders declines were worse and increases less pronounced than estimated, possibly because decline is expected to be greater when measured at a finer resolution (5 km in Flanders; 10 km in Britain)[6,26]. As a test for another taxonomic group, distribution change in rare British plant species was found to be positively related to fractal dimension calculated at scales of 1–10 km or 10–100 km, with a stronger relationship at the finer scale (Supplementary Methods). This suggests that differences in mobility between taxa do not obscure the relationship between aggregation and distribution change; it also supports the notion that the relationship seems stronger when finer-resolution data are used (finer-scale data may be required to detect the relationship in less mobile organisms, for which processes of range change are likely to occur over shorter distances).

Extinction processes typically cause range collapses[10–13], leaving small refuge populations that are prone to extinction from both deterministic and stochastic processes[27]. Consequently, reliable tools are needed to identify range declines and to establish conservation programmes while there remains scope for recovery[27]. We show that current distribution patterns consistently reveal processes of decline and increase, and that species showing the most fragmented patterns for their distribution size have declined the most. Further work is required to confirm whether the relationship is consistent across landscapes and species assemblages, depending for example on trophic group, habitat and dispersal pattern[28], and to assess the coarsest resolution and narrowest geographic extent of distribution data for which the approach is viable. Nevertheless,

analysis of spatial patterns in current species distributions could be a powerful approach for estimating levels of threat for the many regions and taxa with limited information on past distributions and landscape change, or with limited ecological information on species' habitat or climate associations. □

Methods

Distributions

British distribution sizes and fractal dimensions were calculated with the use of all records for each species in England, Wales and Scotland from 1970–82 (ref. 15) and 1995–99 (ref. 16). Occupied 10-km and 100-km squares were calculated with standard Ordnance Survey grid squares. Distribution maps were based on 65,826 species lists (that is, field visits) for 1970–82 (124,978 species × location distribution records), and 437,690 species lists for 1995–99 (1,548,935 records). Changes in distribution size were calculated by randomly resampling the 1995–99 species lists for each 100-km square to equalize recorder effort between the two periods[17]. Proportional change in distribution size was the number of 10-km squares occupied in 1970–82 subtracted from the number of squares occupied in the resampled 1995–99 data, divided by the number of squares occupied in 1970–82.

The analysis includes all resident butterfly species that have regularly been observed in Britain since 1970, apart from those species for which more than 40% of occupied grid squares in either period were migrants, vagrants or deliberate introductions[16]. Fifty-one species were included, none of which occupied 10% or more of their 100-km squares through migrants or introductions[16] (Supplementary Methods).

Area of occupancy and fractal dimension

Area of occupancy (in km^2) of each British species in each period was calculated at two scales, first by summing the areas of occupied 10-km squares, and second those of occupied 100-km squares. Log_{10}AOO at each scale was plotted against log_{10}(side of grid square (in km)), and the fractal dimension (D_{ij}) was the slope of this scale–area curve, subtracted from 2 (ref. 18). The fractal is used in these analyses as a descriptive measurement of spatial aggregation over a narrow range of scales: we do not imply that these species have 'truly' fractal distributions over multiple scales.

Estimating change

To estimate distribution change independently for each British species, 51 linear regressions of distribution change against D_{ij} and AOO (calculated at 10-km scale) were performed, leaving out each species in turn. Coefficients from the analysis with the remaining 50 species were used to estimate change with the use of D_{ij} and AOO for each omitted species. We tested the predictions by using a linear regression of observed change against estimated change for all 51 species (Fig. 2a, b).

Phylogenetic regression

The main results presented refer to linear regressions with species as independent data points, on the assumption that information on phylogenetic relatedness was not available (as might be typical for poorly recorded taxa). We tested the sensitivity of the results to phylogenetic relatedness with GLS regressions[29] implemented in the software package COMPARE[30] (Supplementary Methods). These analyses suggested that the evolutionary constraint acting on distribution pattern, size and change was small, and gave results consistent with those using species as independent data points. For analyses in which the proportion of variation explained is most important, R^2 from the phylogenetic GLS regression is presented alongside the raw results in the main text. Results from all other phylogenetic regressions are presented in Supplementary Information.

Flanders butterflies and British plants

Details of analyses are presented in Supplementary Methods.

Received 23 July; accepted 17 September 2004; doi:10.1038/nature03031.

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Supplementary Information accompanies the paper on **www.nature.com/nature**.

Acknowledgements We thank the contributors to the butterfly and plant distribution surveys in Britain and Flanders; J. Asher and J. A. Thomas for calculating British rates of decline; and M. de la Cruz, A. Escudero, S. Hartley, J. Perry and M. Pocock for assistance with analyses. The work was supported by the UK Natural Environment Research Council. Maps were produced in DMap.

Competing interests statement The authors declare that they have no competing financial interests.

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Identification of human brain tumour initiating cells

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The cancer stem cell (CSC) hypothesis suggests that neoplastic clones are maintained exclusively by a rare fraction of cells with stem cell properties[1,2]. Although the existence of CSCs in human leukaemia is established[3,4], little evidence exists for CSCs in solid tumours, except for breast cancer[5]. Recently, we prospectively isolated a $CD133^+$ cell subpopulation from human brain tumours that exhibited stem cell properties *in vitro*[6]. However,