THE ROYAL SOCIETY

Received 8 October 2002
Accepted 3 December 2002
Published online 9 May 2003

Habitat conversion and global avian biodiversity loss

Kevin J. Gaston[1*], Tim M. Blackburn[2] and Kees Klein Goldewijk[3]

[1]*Biodiversity and Macroecology Group, Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*
[2]*School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*
[3]*National Institute for Public Health and the Environment (RIVM), Department for Environmental Information Systems (CIM), A. van Leeuwenhoeklaan 9, 3720 BA Bilthoven, The Netherlands*

The magnitude of the impacts of human activities on global biodiversity has been documented at several organizational levels. However, although there have been numerous studies of the effects of local-scale changes in land use (e.g. logging) on the abundance of groups of organisms, broader continental or global-scale analyses addressing the same basic issues remain largely wanting. None the less, changing patterns of land use, associated with the appropriation of increasing proportions of net primary productivity by the human population, seem likely not simply to have reduced the diversity of life, but also to have reduced the carrying capacity of the environment in terms of the numbers of other organisms that it can sustain. Here, we estimate the size of the existing global breeding bird population, and then make a first approximation as to how much this has been modified as a consequence of land-use changes wrought by human activities. Summing numbers across different land-use classes gives a best current estimate of a global population of less than 100 billion breeding bird individuals. Applying the same methodology to estimates of original land-use distributions suggests that conservatively this may represent a loss of between a fifth and a quarter of pre-agricultural bird numbers. This loss is shared across a range of temperate and tropical land-use types.

Keywords: birds; global numbers; land-use change; populations

1. INTRODUCTION

The magnitude of the negative impacts of human activities on global biodiversity has been documented at several levels of biological organization. First, changes in the areas of different types of land use have been quantified, particularly a general trend towards replacement of natural vegetation by croplands and pasture, and progressive fragmentation and degradation of those areas of natural vegetation that remain (e.g. Richards 1990; Klein Goldewijk 2001). Second, increasingly concerted efforts have been made to determine the numbers of species that have become globally extinct in recent years, decades and millennia, and trends in these numbers (Smith *et al.* 1993*a*,*b*; Lawton & May 1995; MacPhee 1999), the numbers that are threatened with extinction in the foreseeable future, and the severity of the threats that they face (Heywood 1995; Baillie & Groombridge 1996; BirdLife International 2000). All of these species-level changes follow in major part directly from changing patterns of land use, with, for example, 85% of globally threatened bird species apparently being at risk as a result of habitat loss and degradation (BirdLife International 2000). Third, there have been attempts to estimate the likely magnitude of the loss of genetically distinct populations globally, revealing that in some parts of the world both absolutely and proportionally this may currently be several times greater than the rate of extinction of species (Hughes *et al.* 1997, 1998; Chan 1998; see also Ceballos & Ehrlich 2002).

A logical next step in evaluating the scale of the negative impacts of human activities on biodiversity is to ask to what extent these have reduced global numbers of individuals in major taxa. Changing patterns of land use seem not only to have reduced the diversity of life, but also to have reduced the carrying capacity of the environment in terms of the numbers of organisms that it can sustain (the former losses may follow, at least in part, from the latter; see Remsen 1995; Donald *et al.* 2001). Croplands and pastures, in particular, are structurally greatly simplified compared with many of the land-use types that they have replaced, and a high proportion of their productivity is appropriated directly or indirectly by humans, greatly limiting that available to other forms of life (Vitousek *et al.* 1986; Pimm 2001). As with losses of populations, any systematic losses of numbers of individuals may constitute a potentially insidious erosion of biodiversity, because it may be less apparent and less newsworthy, but carries with it likely reductions in phenotypic and genotypic diversities, and in the capacity to provide ecosystem goods and services (Ehrlich & Daily 1993; Ehrlich 1995; Hughes *et al.* 1997; Ceballos & Ehrlich 2002). However, although there have been numerous studies of the effects of local-scale changes in land use on the abundance of groups of organisms, such as the consequences of different timber extraction regimes for numbers of individual birds (see, for example, Robinson & Robinson 1999; Wardell-Johnson & Williams 2000; Defarrari *et al.* 2001; Lance & Phinney 2001), broader continental or global scale analyses addressing the same basic issues remain largely wanting.

In this paper, we estimate the size of the present global breeding bird population, and then make a crude first

*Author for correspondence (k.j.gaston@sheffield.ac.uk).

© 2003 The Royal Society

Table 1. Estimates of mean bird densities in different land-use types, the pre-agricultural areas of those types and the estimated global numbers of individual breeding birds in each of those types in 1990, the percentage change in numbers of birds between the two land-use states, and the numbers of birds gained and lost by these changes.
(Percentage changes in numbers of individuals cannot be calculated for cropland and pasture, because the numbers have grown from baselines of zero.)

	densities (individuals km^{-2})			area (million km^{-2})		numbers in 1990 (billions)				change in numbers (billions)		
land use	low	'typical'	high	undisturbed	1990	low	'typical'	high	change (%)	low	'typical'	high
cropland	100	300	500	0	14.66	1.47	4.40	7.33	—	+1.47	+4.40	+7.33
pasture	150	375	600	0	30.98	4.65	11.62	18.59	—	+4.65	+11.62	+18.59
ice	0	0	0	2.23	2.23	0	0	0	—	0	0	0
tundra	50	200	350	6.48	6.23	0.31	1.25	2.18	−3.94	−0.01	−0.05	−0.09
wooded tundra	100	250	400	2.70	2.58	0.26	0.65	1.03	−4.25	−0.01	−0.03	−0.05
boreal forest	150	575	1000	17.41	16.77	2.52	9.64	16.77	−3.67	−0.10	−0.37	−0.64
cool conifer forest	350	800	1250	3.59	2.79	0.98	2.23	3.48	−22.37	−0.28	−0.64	−1.00
temperate mixed forest	350	800	1250	6.96	2.96	1.03	2.36	3.69	−57.55	−1.40	−3.20	−5.01
temperate deciduous forest	350	1175	2000	6.09	2.01	0.70	2.36	4.02	−67.02	−1.43	−4.79	−8.16
warm mixed forest	500	1250	2000	6.24	2.52	1.26	3.15	5.04	−59.61	−1.86	−4.65	−7.44
grassland/steppe	100	450	800	18.31	9.25	0.92	4.16	7.40	−49.51	−0.91	−4.08	−7.25
hot desert	50	175	300	20.02	15.87	0.79	2.78	4.76	−20.72	−0.21	−0.73	−1.24
scrubland	600	1000	1400	9.79	2.50	1.50	2.50	3.50	−74.44	−4.37	−7.29	−10.20
savannah	500	850	1200	15.94	8.30	4.15	7.05	9.95	−47.97	−3.82	−6.50	−9.18
tropical woodland	1000	1875	2750	8.20	5.88	5.88	11.02	16.16	−28.32	−2.32	−4.36	−6.39
tropical forest	1500	2500	3500	10.15	8.61	12.92	21.53	30.14	−15.20	−2.32	−3.86	−5.40
total				134.12	134.12	39.34	86.70	134.04		−12.92	−24.53	−36.13

approximation as to how much this has declined as a consequence of land-use changes wrought by human activities. Randomization procedures are employed to provide indications of the robustness of the estimates achieved.

2. MATERIAL AND METHODS

(a) *Data*

Analyses were based on the global areas of 16 different land-use classes (table 1) derived from the History Database of the Global Environment (Hyde v. 2.0) for a period before significant human activity, for the present, and at intervals over the past 300 years. Details of how these estimates were generated are provided in Klein Goldewijk (2001). In brief, the pre-agricultural vegetation patterns—based on climate and soil characteristics—as computed by the BIOME1 model (Prentice *et al.* 1992) were used as a starting point. The areas of human-made agricultural landscapes such as croplands and pastures, were derived from historical inventory data (Mitchell 1993, 1998*a*,*b*; Food and Agriculture Organization 1996) and allocated on top of BIOME's pre-agricultural land cover, with historical human population density maps as the main proxy for these changes; initially it was more likely that agricultural activity occurred in proximity to urban centres rather than in the remote parts of a region. The historical human population density maps were created by downscaling the population density map of Tobler *et al.* (1995), on the basis of historical total population data for several (sub-) administrative units (the largest unit is the country level). Grid cells with the highest historical human population density were classified as most likely available for agricultural expansion at that time. Thus, total population numbers per country (or per sub-administrative unit) are consistent with the statistics, whereas the density patterns reflect the current pattern. The assumption here is that towns/cities did not move spatially during the past 300 years so the distribution of the current density map is also valid for that particular historical time period.

The estimates of current and pre-agricultural land-use class areas are given in table 1, and broadly agree with those generated by other models and measurements. The pre-agricultural undisturbed forest area of 58.6 million km^2 as calculated by Klein Goldewijk (2001) is well within the lower limit of 55.3 million km^2 of Ramankutty & Foley (1999) and the upper limit of 61.5 million km^2 (Matthews 1983). Ramankutty & Foley (1999) used the newly developed, high-resolution (1 km) satellite-based DISCover dataset (Belward & Loveland 1996), whereas Matthews (1983) compiled numerous published sources and satellite imagery, resulting in a potential vegetation map and a separate land-use map with five categories showing varying degrees of cultivation intensity. The cropland estimates range from 14.7 million km^2 (Food and Agriculture Organization 1996; Klein Goldewijk 2001) in 1990 to 20 million km^2 (Ramankutty & Foley 1999). The larger cropland area of Ramankutty & Foley (1999) is owing to the inter-calibration of satellite and statistical data, whereas Klein Goldewijk (2001) relied on just statistical data. Klein Goldewijk (2001) also provides an estimate for pasture, whereas the other studies do not; the 31 million km^2 estimate for 1990 equals the FAO statistics. Richards (1990) shows very little change in the grassland/savannah/pasture area over time. This can partly be attributed to the fact

that large areas of natural grassland have been converted to pasture, with little effect on productivity or carbon fluxes. Klein Goldewijk (2001) estimated an overall increase in the grassland/savannah/pasture area of 4 million km^2, mainly owing to the conversion of pre-agricultural forests to grazing land (e.g. Amazonian pastures for cattle ranching).

Estimates of the current productivity of vegetation for each land-use type (carbon (Pg km^{-2}) in vegetation) were based on those of Houghton (1999), with total carbon (Pg) being the product of this figure and the current land area of the appropriate land-use type.

There is a vast literature on the abundances of breeding birds (e.g. citations in Udvardy 1957; Cramp & Simmons 1977, 1980, 1983; Cramp 1985, 1988, 1992; Wiens 1989; Cramp & Perrins 1993, 1994*a*,*b*; Newton 1998; Gaston & Blackburn 2000). To estimate the total number of individual breeding birds found in the 16 different land-use classes, we first assembled a large collection of papers providing estimates of the total numbers of breeding individuals of all bird species on plots of stated sizes. To the furthest extent possible, we laid emphasis on studies widely acknowledged to be of high quality, sought to maximize the breadth of geographic coverage, concentrated on studies employing territory mapping techniques, employed existing collations of density estimates and avoided studies based on very small census plots (important sources included Wiens & Dyer 1975; Terborgh *et al.* 1990; Wiens 1991; Thiollay 1994; Robinson *et al.* 2000; http://www.cws-scf.ec.gc.ca/canbird/techrep/english/rep_e.htm and references therein). Consulting this set of papers, the first two authors independently derived two estimates for each land-use class, representing low and high *mean* total breeding bird densities (individuals per square kilometre, in steps of 50). Any differences (always small) in these independently derived estimates were then reconciled (usually by employing the more extreme value) to give agreed extreme mean density values for each class. A third, 'typical' density value was then calculated as the mean of the two extremes. The three density estimates for each land-use class are given in table 1.

Inevitably significant biases are likely to remain in these estimates. We highlight three as follows.

(i) How typical are the areas for which published avian density estimates are available is unknown, as is the degree of spatial variation in densities for a given land-use class. Areas chosen for study may well, however, be biased towards higher avian densities; few ecologists intentionally pick 'poor' study sites.
(ii) The frequency and quality of avian density studies from different environments in our sample of the literature (and in the literature at large) was extremely variable.
(iii) Weighing the available evidence to generate estimates of mean density values inevitably involves a marked element of subjectivity.

Throughout, however, we sought to establish extreme mean values between which we can be reasonably confident that the real global mean densities for each class are likely to lie, accepting that all of the figures employed are open to refinement. Randomization procedures (see § 2b) were employed to explore the consequences of the uncertainties associated with the estimates.

For each land-use class, low, typical and high overall breeding bird-population estimates were derived by multiplying the three local density estimates by the area of the appropriate land-use class at a given time. Summing across land-use classes then provided three separate estimates of the global avian population at that time. These figures are based on breeding birds, and would be inflated by non-breeders during the breeding season, and by post-breeding individuals at other times. Seabirds are ignored, as they contribute little to the overall total number of breeding birds (1.2–2.3% of 'typical' estimate of current terrestrial population, see § 3; Shuntov 1974).

(b) *Simulations*

To examine the effects of uncertainty, both in the extent of different land-use classes and in bird densities within each class, three sets of simulations were performed as follows.

(i) We kept the land-use class areas constant (to the values in Klein Goldewijk (2001)) and randomly selected one of the three bird density estimates (low, typical or high) generated for each class (table 1). We used the area and randomly chosen density estimate to calculate the total bird population for each class, and summed these to give the global population estimate. This procedure was repeated to give 5000 such global estimates.
(ii) We kept the bird density estimate constant (the typical estimate for each land-use class was used) and varied the area of each land-use class. Because we do not have an estimate for the error in the class areas calculated from the Hyde database, we assumed that these varied randomly. We calculated the area for each class as the Hyde area estimate plus this estimate multiplied by a random number chosen from a normal distribution with a mean of 0 and standard deviation of 0.25. This generates a distribution of random areas for each land-use class centred on the Hyde estimate, and for which 95% of the areas lie within the range 0.5–1.5 of the actual estimate (the level of agreement between the estimated areas of different land-use types as calculated by Klein Goldewijk (2001) and others (see § 2a), suggests that this is a substantial overestimate of likely levels of error). The random area estimates were constrained to sum to the total ice-free land area of the globe. We achieved this by setting the area of the largest land-use class equal to the total land area minus the sum of all other randomly chosen class areas. All random area estimates were also constrained to be greater than zero. We used the density and randomly chosen area estimate to calculate the total bird population for each class, and summed these to give the global bird-population estimate. This procedure was repeated to give 5000 such global estimates.
(iii) We varied both the bird density and land-use classes at random as described for the first two simulations. We used the randomly chosen density and area estimates to calculate the total bird population for each class, and summed these to give the global bird-population estimate. This procedure was repeated to give 5000 such global estimates. These simulation results were also used to test for the effects of error in the density and land-use class area estimates on estimates of the original global bird-population size (before significant human influence). The randomly assigned areas of crop and pasture land were divided among the remaining land-use classes in proportion to the randomly assigned areas of the natural habitats (very similar results were obtained if this proportion was also chosen

Table 2. Global current bird-population estimates (billions) obtained by applying low, typical and high density estimates to all land-use classes (actual), and from simulations where density (random density), area (random area) and both density and area (random density and area) were varied at random.
(For the simulations, minimum, mean and maximum population estimates and the standard deviation (s.d.) of the estimates, were calculated from 5000 iterations of the procedure. See § 2b for further details.)

	actual	random density	random area	random density and area
minimum	39.34	46.09	65.60	43.97
mean	86.70	86.48	86.71	86.59
maximum	134.04	123.99	107.62	132.52
s.d.	—	12.73	5.40	14.05

at random), to give estimates of the original areas of these classes. These estimates were multiplied by the randomly chosen density estimate for each land-use class to calculate the original bird populations for each, which were summed to give the simulated value for the original global bird-population size.

3. RESULTS AND DISCUSSION

Based on the minimum and maximum estimates derived for bird densities in each of the 16 different land-use classes modelled in the Hyde database, the current global bird-population size is between 39.34 and 134.04 billion individuals (table 1). Using typical average densities for each land-use class gives a total of 86.70 billion individual birds. Previous estimates put the total in the range 100–400 billion (Fisher & Paterson 1964; Wood 1982; de Juana 1992; Gaston & Blackburn 1997), but were based on unexplained methods or much cruder sets of data. Our calculations put the true figure at the lower end of this range. Assuming a human population size of 6 billion, this suggests that there may be an average of fewer than 15 individual breeding birds per person worldwide (for many developed nations the ratio is known to be much lower than this; Gaston 2002).

We tested the sensitivity of the global bird-population estimate to changes in the typical density figures for individual land-use classes by raising or lowering each density estimate by 50%, and recalculating the total. For most land-use classes, this alters the global population estimate by less than 5 billion. The estimate is most sensitive to a 50% change in the bird density value for tropical forests, which gives a 12.5% change in the global population. Thus, our global bird estimates are robust even to quite substantial errors in specific density figures.

More extensive tests of the sensitivity of our estimates to errors are provided by the simulations. These suggest that the range of global bird-population sizes encompassed by our upper and lower estimates is likely to encompass the true value, despite uncertainties in the estimates of bird density and land-use class area. Our actual minimum and maximum density estimates set lower and upper bounds, respectively, on the global population estimates that can be obtained from the simulations where density estimates are chosen at random. The minimum and maximum population estimates from 5000 such simulations both fall inside these limits by several billion individuals (table 2). Most simulated values cluster around the real typical estimate, as might be expected given that land-use classes are assigned minimum and maximum density values at random, and the typical values are means of these extremes. Varying area and using the typical density estimates for each class resulted in simulated global population estimates that cluster even more tightly around the real typical estimate. The minimum and maximum of these 5000 simulations are less extreme than those obtained randomly varying density, and the standard deviation of these simulations is also much smaller (table 2). Randomly varying both the area and density estimates simultaneously produced simulated global population estimates that were similar in all statistics to those obtained just from varying density (figure 1, table 2). Neither the minimum nor the maximum population estimate from these simulations exceeded that obtained by applying the low and high density estimates, respectively, to all land-use classes, and the mean global bird-population estimate from these simulations was still close to the real value calculated from typical density estimates and the areas of different land-use classes from Hyde.

Thus, varying the estimates of the areas of different land-use classes does not add as much variation to the global population estimates as might have been expected. In retrospect, this is perhaps not so surprising. The simulations followed the reasonable assumption that the total area of ice-free land on Earth is constant. Increases in the estimates of the areas of some land-use classes must lead to concomitant decreases in the areas of other classes. These changes will tend, on average, to balance each other, although of course there will be examples of simulations where all increases are in areas of classes depauperate in birds and all decreases in the areas of bird-rich classes (or *vice versa*). As we have no evidence that the true areas of bird-rich land-use classes tend systematically to be overestimated, and those of depauperate classes systematically underestimated, we might expect that errors in the area estimates will to some extent cancel out.

A further check on the accuracy of our figures is possible. Independent estimates of the total bird-population sizes for OECD Europe countries from the European Bird Census Council (BirdLife International/European Bird Census Council (2000) and subsequent revisions) allow us to validate the global population estimate by using our data to predict the numbers expected in these countries according to their land-use composition in the Hyde database. We estimate a total population size for this region of 2.22 (range of 0.81–3.63) billion individuals, which fits well with the upper bound to the range from the EBCC data of 0.91–1.94 billion (range calculated as the sum of the minimum and of the maximum estimates for each

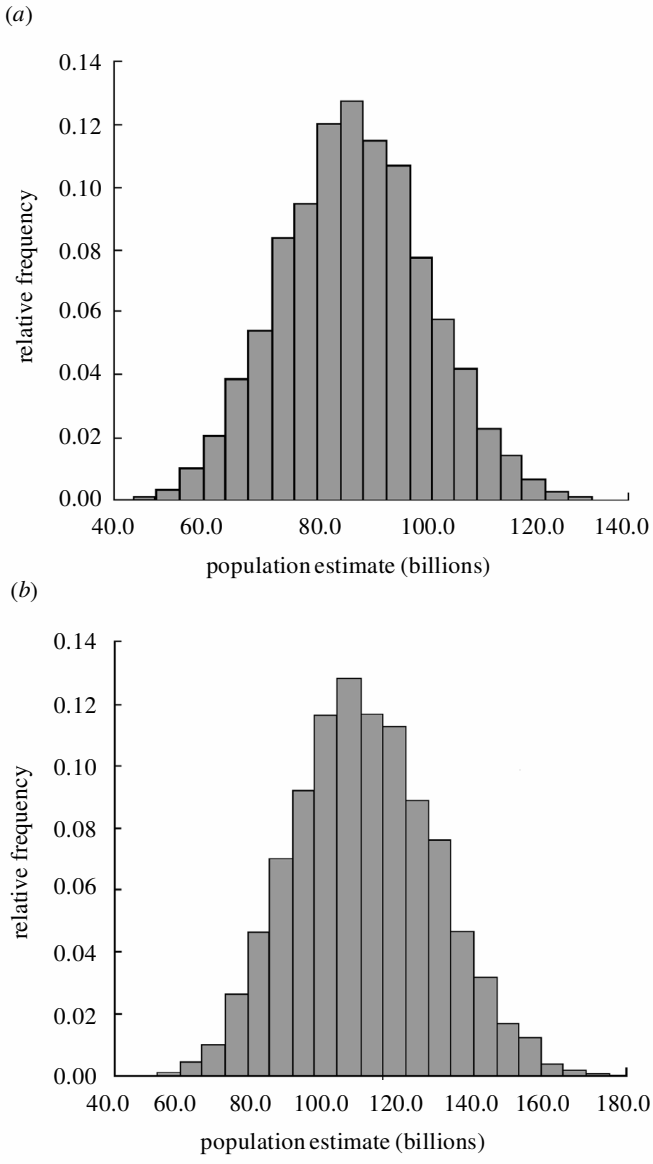

Figure 1. Frequency distributions of 5000 (*a*) current and (*b*) pre-agricultural global bird-population estimates obtained from simulations where both density and area estimates for the different land-use classes were varied at random. See §§ 2b and 3 for further details.

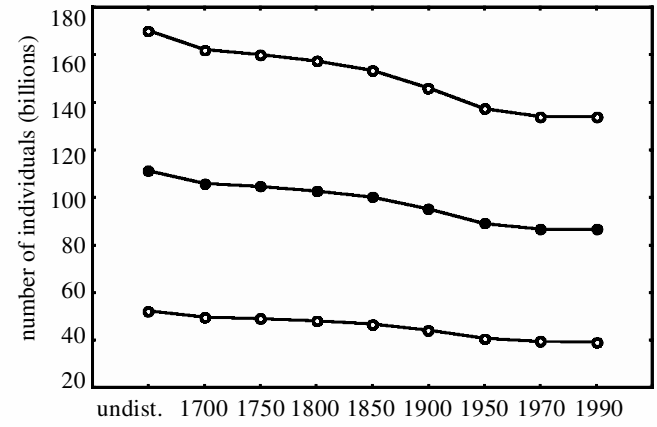

Figure 2. Estimated global numbers of individual birds (in billions) in different periods, based on low (bottom), medium, and high (top) density situations (table 1), beginning with the pre-agricultural pattern of land use.

species; these latter figures exclude introduced species, which would increase them somewhat).

Taking the estimates at face value, a quarter (24.8%; range of 22.5–32.8) of the individuals in the global bird-population estimate inhabit tropical forest, 12.7% (12.1–14.9) inhabit tropical woodland, 11.1% (6.4–12.5) inhabit boreal forest and 8.1% (7.4–10.5) inhabit savannah (table 1). However, 18.5% (range of 15.6–19.3) of bird individuals are estimated to inhabit the human-modified land-use classes of cropland and pasture (table 1). Agricultural lands and their bird populations have expanded in size at the expense of all other land-use classes except ice, and will have led to a concomitant reduction in the numbers of individuals associated with non-agricultural land uses. Estimates from Hyde of the original areas of land-use classes before conversion (table 1) allow us to estimate the original bird populations of these areas, and hence the population changes that land-use conversion has precipitated over time (figure 2). Using typical bird density estimates, this suggests a loss in individual bird numbers of 22.1%. The high and low density estimates for each land-use type bracket the loss within the range 21.2–24.7%. Losses have been particularly severe from temperate deciduous forest, warm mixed forest, grassland/steppe, scrubland, savannah and tropical woodland (table 1).

Our simulations can be used to derive estimates of original global bird populations before significant habitat conversion, and hence to test the effects of errors in density and area figures on our estimates of global population loss. The simulations produced a mean (± standard deviation) original population size of 108.18 ± 19.10 billion birds (figure 1), close to our typical estimate of 111.23 billion (table 1). The minimum and maximum estimates were 51.76 and 174.95 billion, respectively. Subtracting each simulated current population estimate from its corresponding simulated original estimate gave a mean population loss as a result of agricultural habitat conversion of 21.59 ± 10.06 billion birds, compared with our calculated estimated loss of 24.53 billion (table 1). A few of the simulations suggested that agricultural conversion could have led to global population increases: simulated changes ranged from a loss of 63.79 billion to a gain of 6.47 billion birds. However, although population increases are possible, they are exceptional, requiring that the simulations generate a situation of originally high proportions of depauperate habitat across the globe that are converted to more bird-rich agricultural land. Even then, the population gains are relatively small. Experience (and our simulations) tells us that such situations are unlikely to be a true representation of the pattern and effect of global habitat change, even with the uncertainty inherent in our estimates of bird densities and land-use class areas. Most of the simulations (4977/5000 or more than 99.5%) produced estimates of decline.

There are two obvious potential sources of variation in the numbers of individual birds occurring in each land-use type, and hence in the consequences of their transformation to agriculture. First, all else being equal, the number is predicted to increase with available energy/productivity (Wright 1983; Turner *et al.* 1988). However, the relationship between the estimated size of original bird

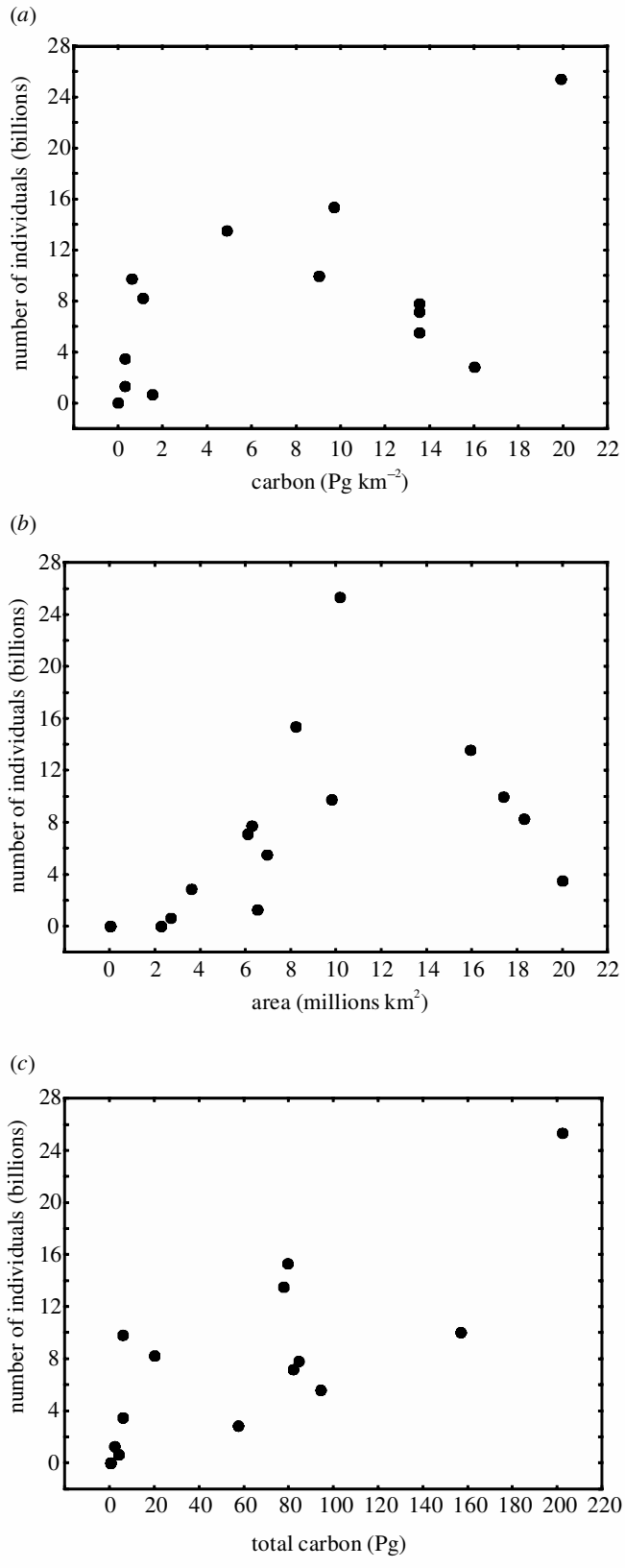

Figure 3. Relationships between the numbers of individual breeding birds estimated to occur in each land-use type before significant human activities (using the 'typical' scenario; table 1), and (*a*) the carbon per unit area in the vegetation of each type ($r = 0.53$, $n = 14$, $p = 0.054$), (*b*) the area of each type (second-order polynomial: $r = 0.77$, $n = 14$, $p < 0.01$) and (*c*) the total carbon in the vegetation of each type ($r = 0.77$, $n = 14$, $p < 0.001$). Cropland and pasture were excluded, as both have areas of zero for original potential vegetation.

populations and productivity is weak (figure 3*a*). This may simply be because, second, the number of birds is also predicted to increase with area (Preston 1948). However, this relationship is actually hump shaped, with smaller original bird populations in small and large areas (figure 3*b*). A third possibility is that area and productivity combined may explain much of the variation in estimated bird numbers. There is indeed a strong positive relationship between the numbers of birds in each land-use type and the total amount of energy available (figure 3*c*).

Our results strongly suggest that bird-population increases from habitat conversion go only a short way towards balancing the associated losses. The net result of agricultural development is a reduction in the capacity of the environment to support biodiversity (figure 2). The total bird-population losses of a fifth to a quarter are smaller than likely species losses to extinction on the same time-scale (8000 species or indigenous populations of land birds are estimated to have been lost from the islands of Oceania alone; Steadman (1995)). The estimated losses of individuals are likely, however, to be conservative, as the activities of indigenous peoples are likely to have affected even otherwise apparently 'pristine' habitats (Grayson 2001), extensive areas of several natural land-use types may have a substantially lowered carrying capacity (e.g. through small-scale habitat fragmentation and degradation, the replacement of natural forest area with plantations: Pimm (2001) and see references in § 1), whereas the mainly migratory breeding populations of relatively pristine high latitude regions (Newton & Dale 1996*a*,*b*) may be affected by the degradation of wintering sites at lower latitudes (Faaborg 2003). Moreover, so far, losses from tropical forests may have been relatively small compared with the numbers of individuals that this habitat type harbours (table 1). Continuing tropical deforestation and transformation to cropland and pasture will result in continuing biodiversity loss in these areas not only by numbers of species and populations, but also by numbers of individuals.

The authors thank R. D. Gregory and the European Bird Census Council for assistance with the data, and J. S. Bale, R. D. Gregory, O. Petchey, S. L. Pimm, D. Storch and two anonymous referees for comments on the manuscript.

REFERENCES

Baillie, J. & Groombridge, B. (eds) 1996 *IUCN red list of threatened animals*. Gland, Switzerland: IUCN.

Belward, A. S. & Loveland, T. R. 1996 The DIS 1 km land cover data set. The International Geosphere-Biosphere Programme: a study of global change (IGBP) of the International Council of Scientific Unions. *Global Change Newslett.* **27**, 7–8.

BirdLife International 2000 *Threatened birds of the world*. Barcelona/Cambridge: Lynx Edicions/BirdLife International.

BirdLife International/European Bird Census Council 2000 *European bird populations: estimates and trends*. Cambridge: BirdLife International.

Ceballos, G. & Ehrlich, P. R. 2002 Mammal population losses and the extinction crisis. *Science* **296**, 904–907.

Chan, K. M. A. 1998 Response. *Science* **280**, 2027g.

Cramp, S. (ed.) 1985 *Birds of the Western Palaearctic*. IV. *Terns to woodpeckers*. Oxford University Press.

Cramp, S. (ed.) 1988 *Birds of the Western Palaearctic*. V. *Tyrant flycatchers to thrushes*. Oxford University Press.

Cramp, S. (ed.) 1992 *Birds of the Western Palaearctic*. VI. *Warblers*. Oxford University Press.

Cramp, S. & Perrins, C. M. (eds) 1993 *Birds of the Western Palaearctic*. VII. *Flycatchers to shrikes*. Oxford University Press.

Cramp, S. & Perrins, C. M. (eds) 1994*a* *Birds of the Western Palaearctic*. VIII. *Crows to finches*. Oxford University Press.

Cramp, S. & Perrins, C. M. (eds) 1994*b* *Birds of the Western Palaearctic*. IX. *Buntings and New World warblers*. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1977 *Birds of the Western Palaearctic*. I. *Ostrich to ducks*. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1980 *Birds of the Western Palaearctic*. II. *Hawks to bustards*. Oxford University Press.

Cramp, S. & Simmons, K. E. L. (eds) 1983 *Birds of the Western Palaearctic*. III. *Waders to gulls*. Oxford University Press.

Defarrari, G., Camilión, C., Pastur, G. M. & Peri, P. L. 2001 Changes in *Nothofagus pumilio* forest biodiversity during the forest management cycle. 2. Birds. *Biodiver. Conserv.* **10**, 2093–2108.

de Juana, E. 1992 Class Aves (birds). In *Handbook of the birds of the world*, vol. 1 (ed. J. del Hoyo, A. Elliott & J. Sargatal), pp. 36–73. Barcelona: Lynx Edicions.

Donald, P. F., Green, R. E. & Heath, M. F. 2001 Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond.* B **268**, 25–29. (DOI 10.1098/rspb.2001.1325.)

Ehrlich, P. R. 1995 The scale of the human enterprise and biodiversity loss. In *Extinction rates* (ed. J. H. Lawton & R. M. May), pp. 214–226. Oxford University Press.

Ehrlich, P. R. & Daily, G. C. 1993 Population extinction and saving biodiversity. *Ambio* **22**, 64–68.

Faaborg, J. 2003 *Saving migrant birds: developing strategies for the future*. Austin, TX: University of Texas Press. (In the press.)

Fisher, J. & Paterson, R. T. 1964 *The world of birds: a comprehensive guide to general ornithology*. London: MacDonald.

Food and Agriculture Organization 1996 *FAOSTAT*. Rome: FAO.

Gaston, K. J. 2002 Abundance, occupancy and conservation biology. In *Avian landscape ecology: pure and applied issues in the large-scale ecology of birds. Proc. 2002 IALE(UK) Conf.* (ed. D. E. Chamberlain & A. M. Wilson), pp. 215–227. Garstang: IALE(UK).

Gaston, K. J. & Blackburn, T. M. 1997 How many birds are there? *Biodiver. Conserv.* **6**, 615–625.

Gaston, K. J. & Blackburn, T. M. 2000 *Pattern and process in macroecology*. Oxford: Blackwell Science.

Grayson, D. K. 2001 The archaeological record of human impacts on animal populations. *J. World Prehist.* **15**, 1–68.

Heywood, V. H. (ed.) 1995 *Global biodiversity assessment*. Cambridge University Press.

Houghton, R. A. 1999 Annual net flux of carbon to the atmosphere from changes in land use 1850–1990. *Tellus* **51B**, 298–313.

Hughes, J., Daily, G. & Ehrlich, P. 1998 Response. *Science* **280**, 2027g.

Hughes, J. B., Daily, G. C. & Ehrlich, P. R. 1997 Population diversity: its extent and extinction. *Science* **278**, 689–692.

Klein Goldewijk, K. 2001 Estimating global land use change over the past 300 years: the HYDE database. *Global Biogeochem. Cycles* **15**, 417–433.

Lance, A. N. & Phinney, M. 2001 Bird responses to partial retention timber harvesting in central interior British Columbia. *Forest Ecol. Man.* **142**, 267–280.

Lawton, J. H. & May, R. M. (eds) 1995 *Extinction rates*. Oxford University Press.

MacPhee, R. D. E. (ed.) 1999 *Extinctions in near time: causes, contexts, and consequences*. New York: Kluwer Academic/Plenum.

Matthews, E. 1983 Global vegetation and land use: new high-resolution data bases for climate studies. *J. Clim. Appl. Meteorol.* **22**, 474–487.

Mitchell, B. R. 1993 *International historical statistics, the Americas: 1750–1988*. London: MacMillan.

Mitchell, B. R. 1998*a* *International historical statistics, Europe: 1750–1993*, 4th edn. London: MacMillan.

Mitchell, B. R. 1998*b* *International historical statistics, Africa, Asia & Oceania: 1750–1993*, 3rd edn. London: MacMillan.

Newton, I. 1998 *Population limitation in birds*. San Diego, CA: Academic.

Newton, I. & Dale, L. 1996*a* Relationship between migration and latitude among west European birds. *J. Anim. Ecol.* **65**, 137–146.

Newton, I. & Dale, L. C. 1996*b* Bird migration at different latitudes in eastern North America. *Auk* **113**, 626–635.

Pimm, S. L. 2001 *The world according to Pimm: a scientist audits the Earth*. New York: McGraw-Hill.

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A. & Solomon, A. M. 1992 A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134.

Preston, F. W. 1948 The commonness, and rarity, of species. *Ecology* **29**, 254–283.

Ramankutty, N. & Foley, J. A. 1999 Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochem. Cycles* **13**, 997–1027.

Remsen Jr, J. V. 1995 The importance of continued collecting of bird specimens to ornithology and bird conservation. *Bird Conserv. Int.* **5**, 145–180.

Richards, J. F. 1990 Land transformation. In *The Earth as transformed by human action* (ed. B. L. Turner II, W. C. Clark, R. W. Kates, J. F. Richards, J. T. Mathews & W. B. Meyer), pp. 163–178. New York: Cambridge University Press.

Robinson, W. D. & Robinson, S. K. 1999 Effects of selective logging on forest bird populations in a fragmented landscape. *Conserv. Biol.* **13**, 58–66.

Robinson, W. D., Brawn, J. D. & Robinson, S. K. 2000 Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecol. Monogr.* **70**, 209–235.

Shuntov, V. P. 1974 *Sea birds and the biological structure of the ocean*. Washington, DC: Bureau of Sport Fisheries & Wildlife, US Department of the Interior & the National Science Foundation.

Smith, F. D. M., May, R. M., Pellew, R., Johnson, T. H. & Walter, K. R. 1993*a* How much do we know about the current extinction rate? *Trends Ecol. Evol.* **8**, 375–378.

Smith, F. D. M., May, R. M., Pellew, R., Johnson, T. H. & Walter, K. S. 1993*b* Estimating extinction rates. *Nature* **364**, 494–496.

Steadman, D. W. 1995 Prehistoric extinctions of Pacific Island birds: biodiversity meets zooarchaeology. *Science* **267**, 1123–1131.

Terborgh III, J., Robinson, S. K., Parker, T. A., Munn, C. A. & Pierpont, N. 1990 Structure and organization of an Amazonian forest bird community. *Ecol. Monogr.* **60**, 213–238.

Thiollay, J.-M. 1994 Structure, density and rarity in an Amazonian rainforest bird community. *J. Trop. Ecol.* **10**, 449–481.

Tobler, W., Deichmann, U., Gottsegen, J. & Maloy, K. 1995 *The global demography project. Technical Report TR-95-6*. Santa Barbara, CA: National Center for Geographic Information and Analysis (NCGIA).

Turner, J. R. G., Lennon, J. J. & Lawrenson, J. A. 1988 British bird species distributions and energy theory. *Nature* **335**, 539–541.

Udvardy, M. D. F. 1957 An evaluation of quantitative studies in birds. *Cold Spring Harbor Symp.* **22**, 301–311.

Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. E. & Matson, P. A. 1986 Human appropriation of the products of photosynthesis. *BioScience* **36**, 368–373.

Wardell-Johnson, G. & Williams, M. 2000 Edges and gaps in mature karri forest, south-western Australia: logging effects on bird species abundance and diversity. *Forest Ecol. Mngmt* **131**, 1–21.

Wiens, J. A. 1989 *The ecology of bird communities*, vol. 1. *Foundations and patterns.* Cambridge University Press.

Wiens, J. A. 1991 The ecology of desert birds. In *The ecology of desert communities* (ed. G. A. Polis), pp. 278–310. Tucson, AZ: University of Arizona Press.

Wiens, J. A. & Dyer, M. I. 1975 Rangeland avifaunas: their composition, energetics, and role in the ecosystem. In *USDA Forest Service General Technical Report WO-1*, pp. 146–181. USDA.

Wood, G. L. 1982 *The Guinness book of animal facts and feats*, 3rd edn. Enfield: Guinness Superlatives.

Wright, D. H. 1983 Species–energy theory: an extension of species area-theory. *Oikos* **41**, 496–506.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.